

SPECIALIZATION FOR VERTICAL HABITATS
WITHIN A CLOUD FOREST COMMUNITY OF MICE

By

CATHERINE ANN LANGTIMM

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To my Dad, who taught me to make my own decisions.

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Abstract of Dissertation Presented to the Graduate School
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By

Catherine Ann Langtimm

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Chairperson: John F. Eisenberg
Major Department: Zoology

In a comparative study of five species of mice inhabiting cloud forest in Costa Rica (Heteromys desmarestianus, Scotinomys teguina, Peromyscus nudipes, Reithrodontomys gracilis, Nyctomys sumichrasti), I examined three aspects of vertical specialization: 1) vertical distribution patterns within the habitat, 2) behavior patterns that result in vertical specialization, and 3) potential selection for cryptic coloration as a consequence of specialization. Mark and recapture trapping that sampled forest floor, understory, and canopy showed that the species were vertically stratified. Trapping during 2.5 years revealed that Heteromys, Scotinomys, and Nyctomys were captured in one stratum, whereas Peromyscus and Reithrodontomys showed a preference for one stratum, but frequented multiple strata. Peromyscus showed a higher frequency of arboreal captures with higher population levels within the community.

In a T-maze experiment conducted at each trap site, a species-typical disposition for a particular stratum was demonstrated that was consistent with the habitat preferences shown during the trapping study. Arboreal species climbed up, while terrestrial species climbed down. The relative strength of that disposition was tested in a Y-maze experiment that placed the preferred direction of escape in opposition

to a difficult escape route. Individuals of the species with generalized behavior more frequently chose the easy escape route, whereas individuals of the specialized species more frequently chose escape to its preferred habitat. Interspecific differences in vertical specialization may be due to differences in a psychological disposition for one stratum and the ability of environmental factors to over-rule that disposition.

Associated with behavioral specialization were differences in pelage color. Arboreal species were more reflective than terrestrial species, which were dark. All species were orange/yellow in hue; arboreal species had high chroma and appeared more orange than terrestrial species which had low chroma and were gray. Two factors affected the calculated appearance of reflectance spectra: the spectral sensitivity of rod cells used in night vision and the color of nocturnal light environments. To nocturnal predators, arboreal species may appear to be a better brightness match to arboreal backgrounds; terrestrial species may appear to be a better match to the dark backgrounds of the forest floor.

CHAPTER 1 INTRODUCTION AND BACKGROUND

Rodents and Ecological Specialization for Vertical Habitats

The New World mice and rats of the family Muridae form a diverse group that most likely originated from an ancestral type that inhabited the tropical forests of North America and whose habits included climbing plants to forage for food (Carleton, 1980; HersHKovitz, 1962). From this origin the group radiated into the diversity of forms known today and can be found throughout the Western Hemisphere in virtually every available habitat--tundra, desert, grasslands, forest, and even tropical streams.

An important process in this radiation was ecological specialization (Eisenberg, 1981). From the general ancestral type that used both forest floor and plants for its activities, individuals, populations, and subsequently species specialized in either arboreal or terrestrial habitats. Arboreal specialization is particularly evident in the Neotropics, which contains the richest and most diverse rain forest rodent fauna of the world and the greatest proportion of mice and rats (family Muridae and Echimyidae) that exploit arboreal habitats (Dieterlen, 1989).

Despite the importance of vertical habitat specialization to the diversification of rodents, we know little about the kinds of adaptations that contribute to an individual's ability to survive and reproduce within specific vertical strata. Locomotor morphology and its effect on climbing performance is the one exception (Brown and Yalden, 1973; Cartmill, 1985; Horner, 1954). Studies based on body structure and principles of biomechanics have shown that certain kinds of

structures enhance the efficiency of locomotion on different types of substrates and reduce the likelihood of falling. Furthermore, there is a strong correlation between morphology and vegetation structure in the preferred habitat of the species (Horner, 1954; Smartt, 1978).

Other adaptations must function as well, but these are less well understood. Various types of behavior, which apparently can evolve independent of locomotor morphology, are important. Layne (1970) felt that "psychological" differences, rather than morphology and ability, were more important in explaining the observed differences in climbing activity of two populations of Podomys floridanus. Thompson (1990) found similar differences among subspecies of Peromyscus maniculatus. Populations significantly differed in the ability to climb a vertical rod, although there were no significant differences in tail or foot length. Differences in climbing disposition also have been demonstrated among captive species and populations of mice by Dewsbury et al. (1980) and Horner (1954). Field studies have demonstrated that behavioral fidelity to a vertical habitat can be affected by various external factors in the environment, but depends on the species. Holbrook (1979) found a shift in arboreal activity of Neotoma stephensi and Peromyscus maniculatus after the removal of Peromyscus boylii, while Harney and Dueser (1987) found no such shift after reciprocal removals of Peromyscus leucopus and Peromyscus maniculatus at a site in Virginia. Evolved behavioral differences were cited as the chief reason for vertical microhabitat segregation in the Virginia community, a greater "arboreal orientation" in P. maniculatus compared to "opportunistic use of arboreal habitats" in P. leucopus.

In addition to behavior, information processing and sensory perception are cited by Futuyma and Moreno (1988) and Endler (1992) as important adaptations that warrant more attention in studies of habitat selection and the evolution of ecological specialization. Species differ in how they perceive the environment and what environmental cues

they use to choose habitats for foraging, reproduction, and evading predation. These differences will affect distribution patterns and ecological interactions, such as intra- and interspecific competition and plant-animal interactions (Partridge, 1978). Small mammals in particular, because of their predominantly nocturnal nature, show behavioral and ecological patterns counter to diurnal faunal groups, suggesting an influence from perceptual abilities. Malcolm (1991b) found that small mammals responded differently to fragmentation than did birds, reptiles, amphibians, or primates in a study of deforestation and fragmentation effects on animal populations in primary forest in Brazil. Many terrestrial and arboreal species of rodents and marsupials, commonly considered primary forest specialists based on distribution patterns in undisturbed habitats, showed increased rather than decreased abundance in secondary forests created by fragmentation. Malcolm cited differences in the way in which the faunal groups perceive and select habitats as the proximate reason for the different responses. He suggested that nocturnal small mammals rely on tactile cues to select habitat for foraging while diurnal animals rely on visual cues. Tactile cues may identify primary and secondary forest as habitats that vary by a small degree whereas visual cues may identify the two as radically different habitats. Additional differences in perceptual abilities that center on vision or olfaction may operate as well and these hypotheses need to be tested.

Within the small mammal radiations, indirect evidence suggests that there are differences in sensory perception between arboreal and terrestrial species that correlate with vertical habitat specialization. Eisenberg and Wilson (1981) hypothesized that rapid locomotion in trees would require the integration of several sensory systems and select for large brain size relative to terrestrial species. They measured brain volume in didelphid marsupials and found a positive correlation between increased size with arboreal preference, but cautioned that K-selection

in complex stable rain forests for features such as longer life-spans and parental care may confound the interpretation. Lemen (1980) found a similar correlation between relative brain size and climbing ability in inter- and intraspecific comparisons of Peromyscus.

Research Overview

I attempted to identify and evaluate some of the behavioral and perceptual features of species that may contribute to vertical habitat specialization in mice, in a field study in Monteverde, Costa Rica. I compared five species that coexisted in the same tract of cloud forest and focussed on two behaviors that I felt may contribute to vertical specialization: 1) behavioral fidelity to one habitat type in spite of fluctuations of biotic and abiotic components of the environment, and 2) the preferred direction of escape of individuals attempting to elude a potential predator. The fidelity study (Chapter 2) was a natural experiment that I ran for 2.5 years and, similar to the removal experiments of Holbrook (1979) and Harney and Dueser (1987), was designed to discern facultative shifts among the species in the use of vertical habitats. The escape response study (Chapter 3) consisted of a series of semi-natural experiments designed to provide data on predator escape behavior, but also, as I will argue later, tested the relative strength of the disposition or tendency to climb.

Adaptations that arise as a result of predation within a particular vertical specialization are not restricted solely to behavior. How visual predators detect and perceive mice within the habitat can drive the evolution of body color and produce morphological adaptations that contribute to crypsis (Cott, 1940; Endler, 1992; Thayer, 1909). Visual perception in predators may be particularly important to the evolution of adaptive coloration in nocturnal mice because of the pronounced physiological differences between color vision and night vision (Lythgoe, 1979). In a final study, I measured and

described pelage coloration in the five species of mice, analyzed the visual match of mice to backgrounds in their habitat, and examined the effect of night vision on color crypsis (Chapter 4).

Terminology

Before proceeding, it is necessary to define some terminology. I use specialization to refer to the terrestrial, arboreal, or semi-arboreal habit of rodent species. These broad categories of ecological specialization are based on substrate use during normal activity patterns; additional ecological specializations in the Mammalia not considered in this research include fossorial, aquatic, and volant (Eisenberg, 1981).

I have assumed that underlying these ecological specializations are behavioral, morphological, and physiological adaptations that evolved under selection pressures encountered as a consequence of long-term utilization of terrestrial and/or arboreal habitats (Futuyma and Moreno, 1988). My primary interest is in the study of these adaptations, but at this stage of the investigation, it is premature and unfounded to call the behavior and color patterns that I studied "adaptations." Heritability and fitness differences within the ecological specialization have not been demonstrated (Endler, 1986a). I have chosen instead to use the term "character," a neutral term from the field of systematics that refers to a basic feature or attribute of an organism that can vary among species or populations, but is common to all the members of the group being considered in comparative analyses. Variants of the character are called "character states" and are described by quantitative or qualitative measures.

The terminology is particularly well-suited for early investigations exploring potential adaptations. The terms "adaptation" and "specialization" have been defined in various ways by various biologists and the use of these terms may connote functions that have

not been adequately demonstrated for the attributes and features being investigated. The terms "character" and "character state" do not necessarily imply an adaptive function, and are amenable to comparative studies, since comparisons are reduced to variants of basic features common to the group as a whole.

Use of the systematic terms also is an acknowledgement and a reminder that phylogeny and historical processes are important components in the evolution of ecological specialization, the evolution of adaptations associated with those specializations, and the adaptive radiation of species (Brooks and McLennan, 1991; Futuyma and Moreno, 1988). This study was not a phylogenetic comparison; however, comparative biology that does not consider possible consequences from phylogeny and descent from a common ancestor can be seriously biased (Harvey and Pagel, 1991). Comparative studies that include from their inception phylogenetic methodology have the opportunity later, as the data base is amassed, to conduct pertinent phylogenetic analyses (for example see Dewsbury, 1972; Langtimm and Dewsbury, 1991).

Research Objective

My primary objective was to analyze behavior and color patterns as potential adaptations that contribute to vertical specialization and to generate hypotheses concerning function that can be tested in future studies with other species in other forest types. Several issues had to be resolved to establish the characters as potential adaptations: 1) Can the characters be measured among individuals and do they represent attributes or features that are typical of the population as a whole and common to all murid species? 2) Do comparisons of characters among species reveal character states that coincide with vertical specialization? 3) Does the character represent a complex of features that may be more easily compared and studied if reduced to its component parts? 4) Within a character state, is there variation, and if so, what

is the nature of that variation? Does it occur among or within individuals and to what extent? Is there evidence that environmental effects in addition to genetic effects contribute to the variation? Particularly with behavioral characters, how plastic is the behavior, and what role may learning or development play? 5) Are there plausible explanations for the function of the character and reasons to expect fitness differences among variants that specialize in different vertical habitats? Can selective factors be identified that may account for the evolution of the character states?

Habitat Description

My study site was located in cloud forest on the Pacific slope of the Cordillera de Tilarán in Monteverde, Provincia de Puntarenas, Costa Rica (10°18'N, 84°48'W). Climate and forest structure in the region are influenced by the northeast trade winds that sweep across the wet Atlantic slope and spill moisture-laden clouds over the continental divide (Lawton and Dryer, 1980). A cloud cap normally sits atop the Cordillera at Monteverde year round. During the rainy season (May to November), clouds and rain originate from convection storms rising from the Pacific, as well as from the northeast trade winds of the Atlantic. The wet season is broken by a brief dry spell, usually in July. During the dry season (December to mid-May), the northeast trades increase in velocity carrying dense mist to the upper elevations and producing a rain shadow in the warmer lower elevations of the Pacific slope. Winds at the continental divide during December through February can exceed 100 kph at canopy level (Lawton and Dryer, 1980). The average yearly rainfall at 1380 m is 2519 mm (data provided by J. Campbell for 1956 through 1990), but is significantly greater at higher elevations. Temperatures can range from a low of 9°C to 26°C.

My study site on the property of John and Doris Campbell is contiguous with the Monteverde Cloud Forest Preserve. Lawton and Dryer

(1980) described the forest as leeward cloud forest, a forest in transition between Tropical Lower Montane Wet and Tropical Lower Montane Rain Forest of the Holdridge life zone system (Tosi, 1969). The canopy is more open than that of a lowland rain forest, and there is a thick subcanopy and understory layer of shrubs. The forest is also smaller in stature; the largest trees range from 25 to 30 m tall and 60 to 90 cm dbh (Lawton and Dryer, 1980). With mist input there is a heavy epiphyte load of herbs, bryophytes, ferns, bromeliads, and woody shrubs. Lianas, however, are not prominent, particularly between tree crowns within the canopy (Lawton and Dryer, 1980).

Species Accounts

Because of Costa Rica's geographic position on the land bridge between the two American continents, the mammal communities at Monteverde consist of South American species that dispersed north, North American species that dispersed south, and several species that originated in situ within Middle America. The rodents particularly are a diverse assemblage because of this dispersion of species during the Great American Interchange (McPherson, 1985; Savage, 1974). This diversity is further influenced by four life zones compressed along the altitudinal gradient of the Cordillera de Tilarán (Tosi, 1969). Within and across those life zones species overlap in various combinations to form a number of communities (Table 1-1).

I focussed my study on five of the most common species of mice in one community in Campbell's Woods. Squirrels and larger rodents were noted on the site (Table 1-1), but not included in the study. Standard museum study-skins, skulls, and electrophoretic tissue samples of voucher specimens are deposited in the Museum of Natural History, University of Kansas, Lawrence, Kansas. Although the five species of mice share the same habitat, they do not share the same life styles,

Table 1-1. Rodent species of Monteverde, Costa Rica. Modified from Hayes and LaVal (1989). Species noted on the study site are indicated by +; the focal species of the study are indicated by ++.

SPECIES	COMMON NAME	LIFE ZONES*

Family SCIURIDAE		
+ <u>Sciurus deppei</u>	Deppe's squirrel	.234
+ <u>S. variegatoides</u>	Variegated squirrel	123.
+ <u>Microsciurus alfaroi</u>	Alfaro's pygmy squirrel	.234
Family GEOMYIDAE		
<u>Orthogeomys cherrei</u>	Pocket gopher	123.
Family ERETHIZONTIDAE		
+ <u>Coendou mexicanus</u>	Prehensile-tailed porcupine	1234
Family DASYPROCTIDAE		
+ <u>Agouti paca</u>	Paca	1234
+ <u>Dasyprocta punctata</u>	Agouti	1234
Family HETEROMYIDAE		
++ <u>Heteromys desmarestianus</u>	Spiny pocket rat	1234
Family MURIDAE		
Subfamily SIGMODONTIDAE		
++ <u>Nyctomys sumichrasti</u>	Vesper mouse	1234
+ <u>Oryzomys albigularis</u>	Tome's rice rat	..34
+ <u>O. alfaroi</u>	Alfaro's rice rat	.23.
<u>O. fulvescens</u>	Pygmy rice rat	.234
++ <u>Peromyscus nudipes</u>	Cloud forest deer mouse	1234
<u>Reithrodontomys creper</u>	Chiriqui harvest mouse	...4
++ <u>R. gracilis</u>	Slender harvest mouse	123.
<u>Rheomys raptor</u>	Goldman's water mouse	..3.
++ <u>Scotinomys teguina</u>	Alston's brown mouse	.234
<u>Tylomys watsoni</u>	Watson's tree rat	1234
Subfamily MURINAE		
<u>Mus musculus</u>	House mouse (introduced)	123.
<u>Rattus rattus</u>	Black rat (introduced)	.23.

* 1=Tropical Premontane Moist Forest, 2=Tropical Lower Montane Moist Forest, 3=Tropical Lower Montane Wet Forest, 4=Tropical Lower Montane Rain Forest, Period(.)=not present in the life-zone.

geographic ranges, or evolutionary history. Four of the five species are members of the subfamily Sigmodontinae in the family Muridae (Carleton and Musser, 1984). The fifth species, Heteromys desmarestianus, is a member of the family Heteromyidae, the pocket mice and kangaroo rats (Hall, 1981).

Nyctomys sumichrasti. The vesper rat is the only extant member of the genus Nyctomys and is generally recognized as one of the most

primitive sigmodontines. Its relationship to the North American or South American radiation of sigmodontines, however, remains enigmatic (Carleton, 1980; Voss and Lindzey, 1981).

The natural history of Nyctomys was studied by Fleming (1970), Genoways and Jones (1972), and Ceballos (1990). Birkenholz and Wirth (1965) studied its growth, development, and behavior in the laboratory. The vesper rat occurs from southern Mexico to eastern Panama and is found in a variety of habitats from dry deciduous to lowland rain forest to cloud forest. The species is nocturnal and arboreal and feeds primarily on fruit.

Scotinomys teguina. Alston's brown mouse is another primitive member of the Sigmodontinae. Its systematic status and relationships are well defined (Carleton, 1980). Hooper and Carleton (1976) studied the biology of Scotinomys both in the field and in captivity.

The genus originated in Middle America and contains only two species. The range of the species is restricted to mid- and high-elevation tropical forests from Chiapas, Mexico, to western Panama. It is crepuscular and diurnal in habit, terrestrial, and predominantly insectivorous, although it also feeds on seeds and fruits. The species reproduces aseasonally and may be monogamous (Hooper and Carleton, 1976).

Reithrodontomys gracilis. The slender harvest mouse is one of several species within Reithrodontomys, a speciose and more derived genus of the Sigmodontinae (Carleton, 1980). The genus was most recently revised by Hooper (1952) and contains two subgenera, the Mexican radiation, Reithrodontomys, and the Central American radiation, Aporodon. The species designation of R. gracilis for the population at Monteverde and a second population on the Atlantic slope at 800 m elevation in the Rio Peñas Blancas valley is provisional. Both populations are outside the present known range of the species and are in atypically wet habitat; R. gracilis previously has not been recorded

from cloud forest and generally occurs in semi-arid and arid areas from the Yucatan peninsula to northeastern Costa Rica. Morphological characters distinguish the Monteverde population as a member of the subgenus Aporodon, but do not unequivocally place it in gracilis. Molecular and morphometric analyses are required to ascertain its systematic definition within the subgenus (M.D. Carleton, pers. comm.). Despite the systematic problems, I use the tentative identification of gracilis when referring to the population of Reithrodontomys at the Campbell's Woods site.

The biology of R. gracilis was reviewed by Young and Jones (1984). The species is nocturnal, and prior to this study no data were available on food habits, behavior, population structure, or other aspects of its natural history (Young and Jones, 1984).

Peromyscus nudipes. The cloud forest deer mouse is one of many species in the diverse radiation of Peromyscus. Its systematic status in Costa Rica is currently uncertain (Carleton, 1989; Timm et al., 1989). Peromyscus nudipes, as defined by Hooper (1968) and Hall (1981), is a high-elevation species restricted to montane forests of Costa Rica and Panama. Huckaby (1980), however, after a morphometric analysis of the mexicanus group of Peromyscus, subsumed the species under the widespread P. mexicanus. Carleton (1989) supported the mexicanus definition until patterns of variation and relationships of Costa Rican and Nicaraguan populations are better understood. However, karyotypic analysis by Stangl and Baker (1984) and Smith et al. (1986) identified a consistent difference in the morphology of the Y chromosome of mexicanus and nudipes that supports a separate species status. The controversy has not been resolved. I follow the nudipes definition that restricts the species to populations in high-elevation Central American wet forest. Since Huckaby (1980) recognized no subspecies in the geographically and ecologically diverse mexicanus, for my purposes

nudipes more accurately identifies the Monteverde population of Peromyscus.

Anderson (1982) studied the population ecology of Peromyscus at Monteverde. He considered the species nocturnal, terrestrial, and omnivorous. Reproduction is suspended during January and February, perhaps as a consequence of reduced food availability during these months of the dry season (Anderson, 1982).

Heteromys desmarestianus. The spiny pocket mouse is the only species I studied in Campbell's Woods that was not a member of the Sigmodontinae. As a member of the Heteromyidae, it is more closely aligned to the pocket gophers than to the murid mice of the Western Hemisphere (Hafner and Hafner, 1983). The family originated in either Central or North America (Wood, 1935). Heteromys is the only genus of the family to contain species that inhabit rain forest. Other members are generally found in dry habitats (Dieterlen, 1989). The systematic status of the desmarestianus species group was recently revised by Rogers and Schmidly (1982) and Rogers (1990). Further revisions are expected.

Population ecology and behavior of H. desmarestianus in lowland Costa Rican rain forest were studied by Fleming (1974a; 1974b) and Fleming and Brown (1975). Behavior in captivity was studied and compared with other rodents by Eisenberg (1963; 1967). Heteromys desmarestianus is nocturnal, inhabits tropical montane wet or lowland rain forests, and ranges from southern Mexico to northwestern Colombia. The species is granivorous and caches seeds. Like all Heteromyidae, H. desmarestianus has fur-lined external cheek pouches that it uses to carry seeds to its burrows. The sexes are dimorphic in size, males weighing about one-third more than females (Fleming, 1974a).

Differences among Species in Locomotor Morphology

The mice I studied at Monteverde all possess very different morphologies that can affect climbing behavior and influence ecological specialization (Table 1-2). The two terrestrial species, H. desmarestianus and S. tequina, show morphologies considered to be specializations for speed and efficiency in terrestrial locomotion (Cartmill, 1985; Brown and Yalden, 1973). The hind foot is long and narrow, increasing the effective length of the leg and consequently, the length of stride (Brown and Yalden, 1973). The claws are straight, reducing the likelihood of catching on the substrate as it runs. The basic gait of Scotinomys involves a diagonal pattern of limb coordination in which a forelimb and the alternate hind limb move in synchrony. In Heteromys, however, locomotion is by quadrupedal saltation in which the forelimbs move in synchrony and alternate with the synchronous movement of the hind limbs. This type of locomotion is generally found in species with greater speed. Scotinomys tequina has a short tail, but H. desmarestianus has a tail that is quite long, a feature commonly found in climbing and hopping species and used for balance and/or support (Cartmill, 1985; Horner, 1954). However, the attachments between the tail vertebrae of H. desmarestianus are weak. Although a potentially useful feature when the tail is grabbed by a predator, the weak ligatures limit the usefulness of the tail for support while climbing.

In contrast, the other species show morphologies considered more efficient for climbing. In R. gracilis, the hind foot is broad and foot pads are prominent with numerous papillae, increasing the frictional surface of the sole of the foot for stability on curved branches. The claws are recurved to facilitate clinging to vertical and inclined surfaces (Cartmill, 1974). The tail is longer than the head and body, and the extreme tip of the tail is semi-prehensile. Nyctomys sumichrasti shows similar arboreal adaptations in the hind foot, but its

Table 1-2. Comparison of adult external measurements of the five species studied in Monteverde.

SPECIES	WEIGHT (g)	HEAD & BODY LENGTH (mm)	TAIL LENGTH (mm)	HIND FOOT LENGTH (mm)
<u>Reithrodontomys gracilis</u>	8-14	61-80	104-124	18-21
<u>Scotinomys teguina</u>	9-16	72-83	50-60	17-20
<u>Peromyscus nudipes</u>	35-57	114-130	106-140	25-29
<u>Nyctomys sumichrasti</u> *	38-67	99-140	102-157	20-27
<u>Heteromys desmarestianus</u>	80-105	133-149	130-190**	35-40

*from Emmons (1990)

**from Hall (1981)

tail is thicker and shorter without a prehensile tip. Short hairs on the thick tail may increase friction and reduce slipping while ascending inclined substrates (Cartmill, 1974). Peromyscus nudipes has a generalized morphology intermediate to terrestrial and arboreal species that is adequate for climbing.

Ecological Differences from Forest Floor to Canopy

Differences in biotic and abiotic factors in the habitat can be found among the forest floor, the lower understory, and the canopy of the Monteverde cloud forest that not only can promote vertical specialization, but also select for adaptations associated with specialization. Spatial differences in these factors describe microhabitats and ecological niches that species can exploit. In forests, these microhabitats are compressed into only 25 to 100 m along the vertical dimension, whereas they may extend for kilometers across the horizontal dimension. In evergreen tropical forests, there is no seasonal period of dormancy from cold weather as in temperate forests; food and cover from predators are abundant and relatively constant throughout the year. These conditions facilitate arboreal specialization and are cited by Dieterlen (1989) as the major factor contributing to the richness of species of rodents found in tropical rain forests.

Trophic resources. Seasonal or chronic patterns of low food resources on the forest floor has been invoked by previous investigators as an assumed factor influencing the evolution of climbing behavior in small mammals (Horner, 1954; Layne, 1970; Smartt, 1978; Thompson, 1990; Verts et al. 1984). Many plant species in the Monteverde area produce fruits that could be consumed by frugivorous, omnivorous, or granivorous rodents. These fruits vary in size, nutritional value, display, and vertical distribution (Dinerstein 1983, 1986; Koptur et al., 1988; Wheelwright et al., 1984). There is also marked variation among years

and between wet and dry season in fruiting phenology. Koptur et al. (1988) found that shrubs and treelets had a moderate peak in fruit production during the first half of the year (wet season and early dry season). Bimodal fruiting patterns were seen in plants fed on by frugivorous bats (Dinerstein 1983; 1986), with peaks at the dry/wet season transition and the late wet season.

Rodents are not known to specialize on flower resources; however, mice are generally opportunistic foragers, and species that climb most likely supplement their diet with nectar, pollen, or flower parts. Lumer (1980) found several species of mice, including one of my study species, P. nudipes, feeding on the nectar of Blakea chlorantha, a hemi-epiphyte growing on the Continental Divide above Monteverde.

Numerous rain forest rodents feed on invertebrates when available (Dieterlen, 1989). Nadkarni and Longino (1990) compared the macroinvertebrate faunas in ground and canopy leaf litter and humus at Monteverde and found that both strata shared a similar invertebrate community comprising Acarina (mites), adult Coleoptera (beetles), holometabolous insect larvae, Formicidae (ants), Collembola (spring-tails), and Crustacea (amphipods and isopods). Annelids were absent from all the samples, but this may have been an artifact of their techniques. Abundance was greater on the forest floor, with a mean density 2.6 times greater than in the canopy. The vertical distributions of flying insects has not been examined at Monteverde, but differences among forest floor, understory, and canopy have been documented at other sites in tropical forests (Sutton, 1989).

When and where mice climb to forage for fruits, flowers, and invertebrates depend on a number of factors. Accessibility of the resource within the plant (Denslow and Moermond, 1982), climbing ability of the mouse (Horner, 1954; Layne, 1970), nutritional needs (particularly during reproduction/lactation [Bronson, 1989] or periods of resource limitations [Verts et al., 1984]), and intra- or

interspecific competition (Holbrook, 1979) can affect climbing behavior and vertical habitat specializations.

Predators. Predation has been shown to be a strong selective agent for habitat specialization across the landscape in terrestrial populations of mice (Kotler, 1984). Similar selection may operate for the evolution of vertical habitat specialization as well. A diversity of vertebrate predators that feed routinely or occasionally on mice inhabit the cloud forest of Monteverde (Table 1-3). These include numerous species of snakes, birds, and large mammals. The different classes of predators employ a range of sensory modes to detect prey. Vision and hearing are the primary modes for birds, while mammals rely on olfaction, hearing, and vision, and snakes use vision and the sensation of vibrations or infrared radiation. The predator species also vary in locomotion, the vertical strata and time of day in which they most frequently forage, and search and attack behavior.

Forest structure. The physical structure of forests varies vertically. At Monteverde, Pounds (1988) studied the effects of this variation on vertical distributions and behavioral and morphological specializations among climbing species of Anolis lizards. Greater stem lengths and widths, as well as greater distances between branches and stems, were correlated with height in the understory (up to 6 m). The Anolis species within the community were vertically stratified along this gradient, and behavior and morphology were correlated with patterns expected to evolve based on first principles of biomechanics in locomotion (Cartmill, 1985). Similar evolutionary processes affect all quadrupedal vertebrates, including climbing mice and rats (Horner, 1954; Smartt, 1978).

Table 1-3. Vertebrate predators known to occur in the Monteverde area. Species list modified from Hayes et al. (1989), Law (1988), Hayes and Laval (1989).

SPECIES	LIFE-STYLE*

Mammalia	
Marsupialia	
<u>Didelphis marsupialis</u>	Scansorial
<u>Philander opossum</u>	Terrestrial
<u>Caluromys derbianus</u>	Arboreal
<u>Marmosa alstoni</u>	Scansorial
<u>M. mexicana</u>	Scansorial
Chiroptera	
<u>Vampyrus spectrum</u>	Volant
<u>Trachops cirrhosus</u>	Volant
Primates	
<u>Cebus capucinus</u>	Arboreal
Carnivora	
<u>Urocyon cinereoargenteus</u>	Terrestrial
<u>Mustela frenata</u>	Terrestrial
<u>Eira barbara</u>	Scansorial
<u>Conepatus semistriatus</u>	Terrestrial
<u>Procyon lotor</u>	Scansorial
<u>Nasua narica</u>	Scansorial
<u>Potos flavus</u>	Arboreal
<u>Bassaricyon gabbii</u>	Arboreal
<u>Felis concolor</u>	Terrestrial
<u>F. onca</u>	Terrestrial
<u>F. pardalis</u>	Scansorial
<u>F. weidii</u>	Scansorial
Aves	
Accipitridae	
<u>Elanoides forficatus</u>	Volant
<u>Chondrohierax uncinatus</u>	Volant
<u>Accipiter bicolor</u>	Volant
<u>A. striatus</u>	Volant
<u>A. cooperii</u>	Volant
<u>Buteo jamaicensis</u>	Volant
<u>B. albonotatus</u>	Volant
<u>B. swainsoni</u>	Volant
<u>B. platypterus</u>	Volant
<u>Leucopternis princeps</u>	Volant
<u>Harpyhalietus solitarius</u>	Volant
<u>Spizaetus ornatus</u>	Volant
<u>S. tyrannus</u>	Volant
Falconidae	
<u>Micrastur ruficolis</u>	Volant
Tytonidae	
<u>Otus clarkii</u>	Volant
<u>Pulsatrix perspicillata</u>	Volant
<u>Ciccaba virgata</u>	Volant
<u>C. nigrolineata</u>	Volant
Reptilia	
Colubridae	
<u>Chironius exoletus</u>	Scansorial
<u>Clelia scytalina</u>	Terrestrial
<u>Dendrophidion paucicarinatum</u>	Scansorial
<u>Drymarchon corais</u>	Terrestrial
<u>Drymobius margaritiferus</u>	Terrestrial

Table 1-3 continued

SPECIES	LIFE-STYLE*
<u>Erythrolamprus vizonus</u>	Terrestrial
<u>Geophis brachycephalus</u>	Terrestrial
<u>G. godmani</u>	Terrestrial
<u>Lampropeltis triangulum</u>	Terrestrial
<u>Leptophis nebulosus</u>	Scansorial
<u>Liophis epinephalus</u>	Terrestrial
<u>Masticodryas melanolomus</u>	Terrestrial
<u>Ninia psephota</u>	Terrestrial
<u>Oxybelis fulgidus</u>	Arboreal
<u>Senticolis triaspis</u>	Scansorial
<u>Sibon annulata</u>	Arboreal
<u>S. dimidiata</u>	Arboreal
<u>Trimetopon gracile</u>	Terrestrial
<u>T. pliolepis</u>	Terrestrial
<u>T. simile</u>	Terrestrial
Elapidae	
<u>Micrurus nigrocinctus</u>	Terrestrial
Viperidae	
<u>Bothriechis lateralis</u>	Arboreal
<u>B. nigroviridis</u>	Arboreal
<u>B. schlegelii</u>	Arboreal

* arboreal=forages primarily in plants; scansorial=forages on the ground as well as in plants; terrestrial=forages primarily on the ground; volant=forages on the wing.

Vertical structure above 6 m has not been studied at Monteverde, but at other sites marked differences have been found. Biomass estimates reveal vertical patterns in the distribution of leaves and wood. Leaf biomass in a Malaysian rain forest was found at 5 to 10 m above the forest floor to decrease in relation to the low understory, and then increase with height in the upper understory and lower reaches of the canopy (Kira and Yoda, 1989). Wood biomass of tree and shrub stems was greatest in the lowest strata, decreasing steadily with ascent in height, while the biomass of branches and liana stems showed a similar pattern, but not such a sharp rate of decrease. The asymmetric distribution of green leaves and brown bark within the forest has implications for the conspicuousness of mammals against the color background of the habitat (Endler, 1978).

Temperature, rainfall, and humidity. Rainfall in the Monteverde area shows marked seasonal amplitudes (Figure 1-1), while temperature maxima and minima show less seasonal variation (Figure 1-2), a pattern common to moist tropical climates (Richards, 1952). Vertically within the forest these factors show marked gradients. Nadkarni and Longino (1990) cited unpublished climatic data collected in Monteverde on differences between the forest floor and canopy. They describe the canopy as experiencing more wind and mist, higher temperatures, and a greater frequency of wet/dry cycles. Quantitative studies in other tropical forests show that the forest floor is relatively insulated by the canopy from the effects of wind, solar radiation during the day, and radiative cooling at night (Kira and Yoda, 1989; Longman and Jenik, 1974; Richards, 1952).

Light. Ambient light varies between forest floor and canopy not only in intensity, but in color composition as well. Both properties of light can affect the conspicuousness of prey to predators against the background of the habitat (Endler, 1991; 1992). Henry Gholz (pers. comm.), working in the Monteverde Cloud Forest Preserve (MVCFP), found that photosynthetically active radiation (PAR) 5 m below the canopy averaged only 5% of incident PAR striking the canopy. Endler (in press), measuring the spectral composition of light along the length of a tower in rain forest on Barro Colorado Island, Panama, found that ambient light under clear conditions changed from blue-gray to green in the descent to the forest floor.

The spatial differences in biotic and abiotic factors among the forest floor, the lower understory, and the canopy of the Monteverde cloud forest describe microhabitats and ecological niches that species can exploit. These differences will influence vertical distribution patterns. However within a stratum, these factors can vary on a temporal basis (day to night, season to season, and year to year) and can influence when individuals use a microhabitat. Where and how often

individuals climb can affect ecological specialization and is the topic of the following chapter.

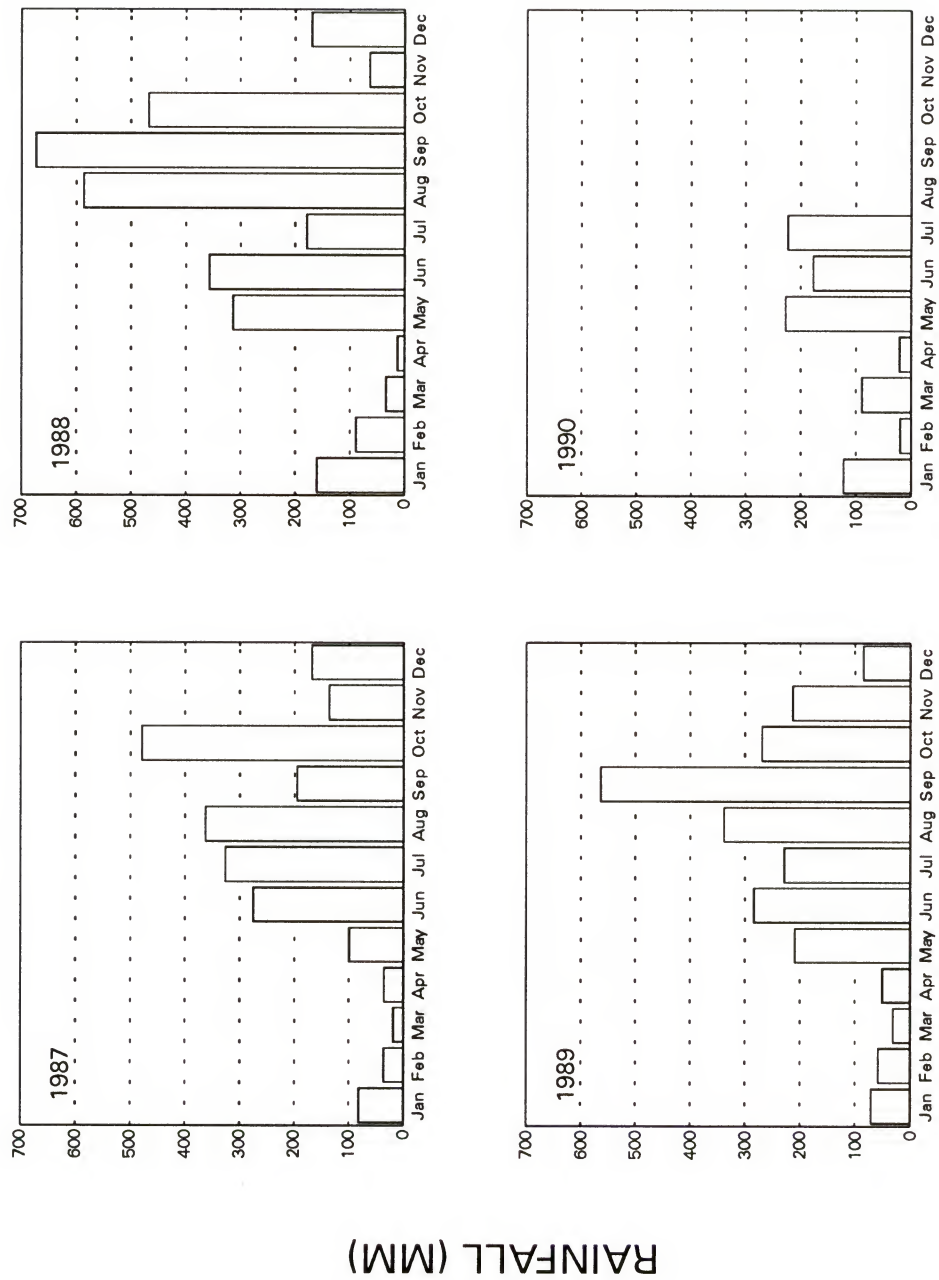


Figure 1-1. Monthly rainfall in Monteverde, Costa Rica, January 1987 through July 1990. Data provided by John Campbell

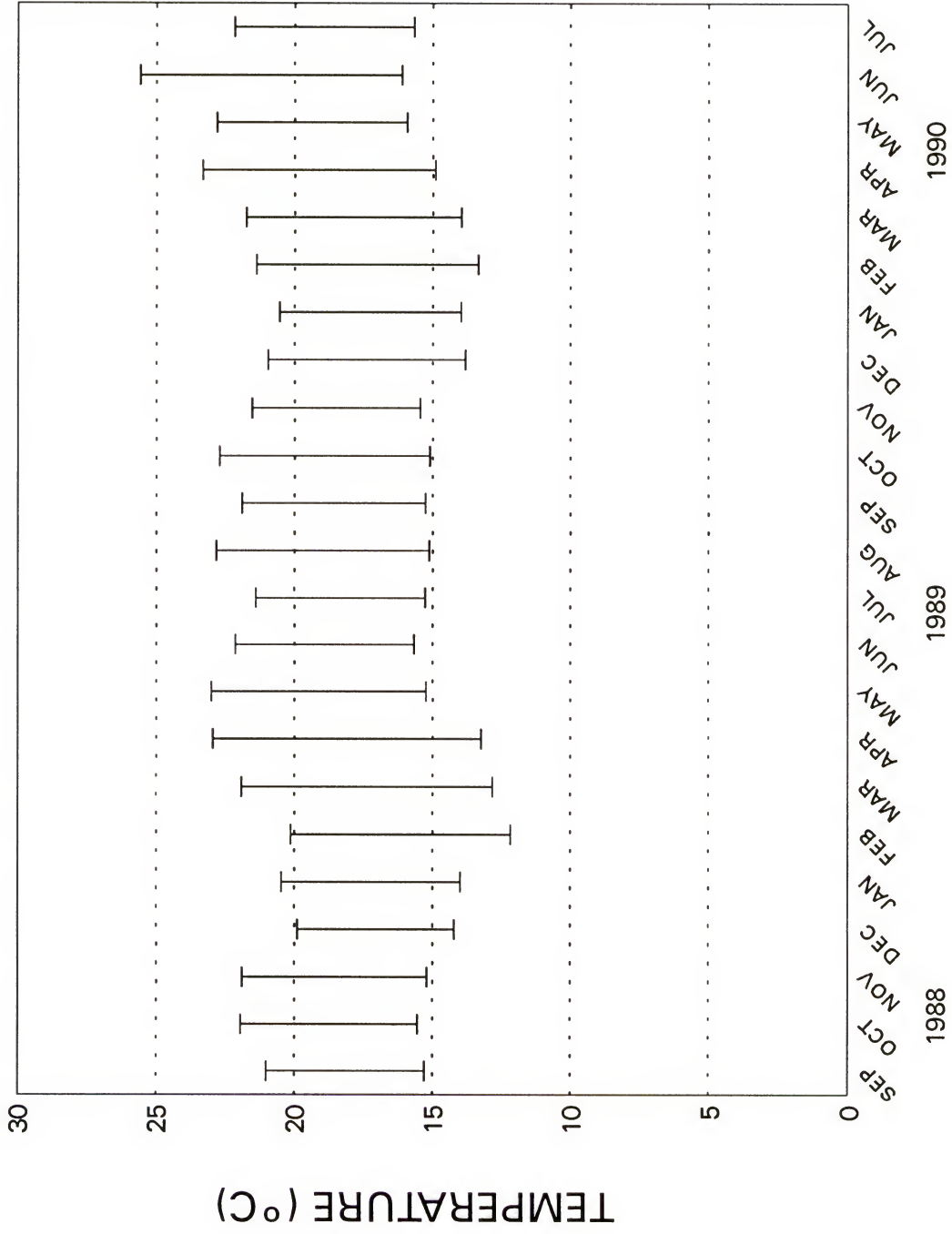


Figure 1-2. Average monthly maximum and minimum temperatures in Monteverde, Costa Rica, September 1988 through July 1990. Data provided by John Campbell

CHAPTER 2
VERTICAL DISTRIBUTION PATTERNS AND
FIDELITY TO VERTICAL STRATA

Introduction

Mice vary in climbing behavior, both individually and among species (Horner, 1954; Thompson, 1990). Eisenberg (1978) described a continuum of species that grades from the terrestrial that never, or only infrequently climb, to the scansorial or semi-arboreal that often climb, to the arboreal that rarely descend to the ground. Not only do individuals and species differ as to when they climb, but field studies show that often they are vertically stratified in the habitat as well (Ceballos, 1990; Genoways and Jones, 1972; Harney and Dueser, 1987; Malcolm, 1991a, 1991b).

This variation in climbing behavior has important implications for specialization and the evolution and maintenance of adaptations in vertical habitats, since selective regimes are encountered as a consequence of when and where individuals climb. The direction of evolution will be determined by the selective forces within the strata (Endler and McLellan, 1988), while the strength of selection will depend in large part on the degree of fidelity individuals in the population have to a particular stratum. Strong fidelity will promote specialization via the action of one selective regime that can select for behavioral, morphological, and physiological characters that function best in that particular stratum. Relaxed fidelity and the frequenting of several strata during daily, seasonal, or life-long activities will promote generalization via the action of more than one selective regime that can influence the evolution and maintenance of characters that are either polymorphic within the population or display

some plasticity or range of expressions and functions within the individual (Futuyma and Moreno, 1988). Fidelity to a particular vertical stratum, therefore, is a behavioral character that appears to be an important component of vertical specialization.

A first step in measuring and describing this character for each of the species in the Monteverde rodent community was determining what vertical strata the mice frequented and how strong was each population's association with those strata during naturally occurring changes in the environment. The generally nocturnal and cryptic nature of mice made direct field observation of climbing activity difficult, particularly in the higher strata of the forest. However, vertical distribution patterns could be approximated from a long-term mark and recapture trapping study. Trapping, in contrast to tracking techniques, allowed me to monitor individual mice in large enough numbers over a sufficient period of time to make inferences about vertical distribution patterns within the populations. Temporal changes in the proportion of each population captured in ground and arboreal traps during the 2.5 year study were used as indices of fidelity to a particular stratum. I tested for consistency in capture frequencies of individuals among strata over 24 hours, over monthly trapping sessions, and between years.

I trapped in three vertical strata: forest floor, lower understory, and canopy. These strata differ markedly in several abiotic and biotic factors that can influence natural selection, and that change in the cloud forest from day to night, season to season, and year to year. I focussed on differences in the capture of individuals on the forest floor and in the lower understory primarily because of the sharp interface of terrestrial and arboreal habitats (and consequently maximizing the potential for sharp changes in selective regimes). In contrast, the understory and canopy show a gradation from one stratum to the other, making it difficult to monitor changes in the vertical distribution of individuals and to characterize fidelity to one or the

other stratum. I therefore did not trap on a regular basis in the canopy and only used capture data from that stratum to document the presence or absence of species in the canopy.

Materials and Methods

General

I employed two separate three-dimensional trapping designs: one to sample the forest floor and lower understory and a second to sample within the canopy and upper heights of the understory. In the understory I trapped monthly from February to July, 1987, and at irregular intervals from September, 1988 to August, 1990 (Table 2-1). I trapped in the tree crowns during two separate sessions in 1987 and 1989. A trapping session for both designs typically ran for three consecutive days, but sometimes longer depending on weather, the condition of the traps (mold was a problem during the rainy season), and the sampling protocol of the experiments performed in conjunction with the trapping (See Chapters 3 and 4).

I captured animals in Sherman live-traps baited with a dry mixture of rolled oats, peanut butter, and banana to attract granivorous, frugivorous, and omnivorous species. All traps were checked daily for captures in the early morning. I processed and released all captured animals on-site. I washed traps with water and a stiff brush between sessions. To identify individuals, I marked each animal on the ear with a unique number. During the initial study in 1987, I marked individuals by clipping a sequence of toes, but because the toe clips could affect climbing behavior I changed to ear marks. For the larger species (P. nudipes and H. desmarestianus) I used a #1 metal ear tag from the National Tag Company. The numbered tag was punched through the external pinna with pliers made for this purpose, also from the National Tag Company. Smaller species (R. gracilis and S. teguina) routinely tore

off the tag, so I identified these with a pattern of cut notches in the ear.

Table 2-1. Dates and duration of the trapping sessions. ** Indicates trapping sessions in the crowns of canopy trees.

Year	Dates	Duration (days)	Season
1987	26-28 Mar	3	Dry
	25-29 Apr	5	End of dry
	29 May - 02 Jun	5	Wet
	21-24 Jun	4	Wet
	15-18 Jul	4	Wet
**	02-11 Jul	7	Wet
1988	04-06 Oct	3	Wet
	16-18 Nov	3	Wet
1989	14-16 Jan	3	Dry
	17-21 Feb	4	Dry
**	08-14 Mar	6	Dry
	09-11 May	3	Begin wet
	16, 18, 19 Jun	3	Wet
	26, 29 Jun & 4, 5 Jul	4	Wet
	09-11 Sep	3	Wet
1990	09-11 Jan	3	Dry
	06, 15 Mar	2	Dry
	18-20 May	3	Wet
	11, 21 Jul	2	Wet

I recorded the following data for each animal: site and date of capture, species, sex, weight, age class based on pelage color and size (adult, subadult, juvenile), and reproductive condition (males: abdominal or descended testes; females: size of nipples, presence or absence of lactation, possible pregnancy).

Trapping within the Understory

To quantify the frequency of occurrence of individuals of each population on the forest floor and in the lower understory, I ran a transect that consisted of 25 trap stations set approximately 20 m apart along a 500 m segment of a foot-trail. At each station I placed traps at two heights. The upper traps were 1-2 m above the forest floor and were tied onto branches of shrubs, vines, trunks of large trees, or fallen branches and trees (hereafter referred to as arboreal traps).

The lower traps were on the forest floor, directly beneath the arboreal traps. The close proximity of the understory traps to the forest floor allowed me to assess minor changes in the vertical distribution of individuals that may only occasionally climb to low heights in the forest.

Proximity, however, also increased the probability of an animal encountering a closed trap and being baited by odor to a stratum that it normally would not frequent. A baiting effect was demonstrated in a previous study of microhabitat selection in terrestrial mice (Douglass, 1989). To minimize this bias, in the analysis I only included those captures in which a trap was open at the adjacent height, indicating that the animal had had the opportunity to enter a trap at the other stratum. During the first two months of trapping I had multiple captures at stations on the first half of the transect, with few capture data meeting the criterion for analysis. To increase the sample, I set two traps within 1.5 m (but normally less than 0.8 m) of each other in each stratum at each of the first 13 stations. I reasoned that an animal was more likely to search first the immediate area within a stratum where it first encountered a closed trap with the smell of food than to switch to a "new patch" in another stratum that held no such indication of possible foraging success (see Krebs, 1978). On the latter half of the transect there were fewer multiple captures at a station with a greater proportion of the capture data meeting the analysis criterion. I therefore set only one trap at each height on the remaining 12 stations.

To quantify circadian patterns in capture frequency, I left the traps open continuously over six consecutive days during the March 1987, trapping session. I checked the traps at 0700, 1030, 1230, 1430, and 1630 h. Based on the high percentage of captures after sunset (see Results), in subsequent trapping sessions I closed the traps during the day and opened and rebaited them during the late afternoon.

Trapping within Tree Crowns

To quantify the frequency of occurrence of individuals in the upper understory and the canopy, I trapped at three heights in six canopy trees. I chose two trees adjacent to the understory transect in Campbell's Woods and four trees in similar leeward cloud forest at a site 2 km distant in the Monteverde Cloud Forest Preserve (MVCFP). I used five criteria to select trees for sampling: 1) the tree crown contributed to the canopy of the forest, 2) the crown contained a diversity of epiphytes, vines, and climbing substrates that might contribute to food resources and nest sites of arboreal mice, 3) branches, vines, and/or lianas were present on the tree trunk and provided suitable substrates to tie traps below the crown, 4) crowns were accessible using single-rope climbing techniques, and 5) several branches within the crown provided a platform and tie-in points from which I could safely maneuver and set traps.

I placed five traps at each of three heights in each tree. Multiple traps at each height allowed me to determine if more than one individual or species was active at each stratum in the same tree on the same night. However, multiple traps at each height could contain individuals before they had the opportunity to move to strata where they normally are active. In instances where a species was only trapped at one height, suggesting free movement may have been restricted by trap placement, I tested for the effect by eliminating the traps at that height.

I placed the first set of traps directly on the ground, encircling the base of the tree. A second layer of traps, on vines and branches, encircled the trunk mid-way to the crown, 6 to 10 m above the forest floor. Traps placed on vines against the trunk were oriented such that the trap treadle was horizontal and an animal could climb into a trap from the side and trigger the door as it jumped to the trap floor. In

the crown, a third layer of traps was tied on branches and lianas, 13-19 m above the forest floor.

Because of the difficulty of ascending into the crown, I left the traps open for the entire trapping session and checked the traps once each morning. To reduce the need to rebait daily, I suspended bait, tied into a small cloth bag, from the closed back door of the trap (Malcolm, 1991a). Bait within the bag was relatively impervious to foraging ants, did not gum up the trap, and was not washed away by rain. Mice, however, could detect the bait by smell and easily gnawed through the cloth to feed during a night in the trap.

Analyses

Previous trap encounters can bias capture frequencies. Some individuals will readily reenter traps ("trap happy"), while others avoid traps and subsequent recapture ("trap shy"). Considering all captures in statistical analyses could over-represent the behavior of a few individuals and not give a clear picture of distribution patterns in the entire population. To control for this effect, I analyzed first-captures of individuals separately from recaptures.

I tested for consistency in capture among strata with a chi-square test. In instances where sample sizes were small and the expected frequency fell below five, I calculated Fisher's Exact Probability using SAS (SAS Institute Inc., 1987).

Facultative changes in vertical distribution can be affected by population density. My trapping design was not appropriate for an accurate estimation of densities. Instead, I calculated the minimum number of individuals known to be alive on the transect during each trapping session and used it as an index of population levels (Krebs, 1966; Seber, 1982). The value was calculated by direct enumeration (Krebs, 1966), adding the number of individuals captured during the

trapping session to the number of individuals not trapped but known to be alive as a result of capture at a later date.

Results

Vertical Distribution Patterns

During the 2.5 year study in the understory of Campbell's Woods, I trapped 104 different individuals of eight species. Trapping frequencies at each of the two heights in the understory indicate species-typical patterns in vertical distribution (Table 2-2). Of the five most common species, H. desmarestianus and S. tequina were never found off the forest floor. Nyctomys sumichrasti, in contrast, was only captured in arboreal traps. This species was uncommon and only one individual of five was recaptured after it was initially marked and released. Reithrodontomys gracilis and P. nudipes were taken both in ground and arboreal traps. However, the frequencies of capture between the strata differed significantly from a 1:1 ratio. Reithrodontomys gracilis was most frequently captured in arboreal traps, whereas P. nudipes was taken most frequently in ground traps.

Species-typical patterns in vertical distribution were also evident in the trapping frequencies in the crowns of canopy trees (Table 2-3). Reithrodontomys gracilis and N. sumichrasti were the only species trapped above 3 m. Only one individual of N. sumichrasti was captured, but R. gracilis was more abundant in the upper and midlevel heights of the forest (Table 2-3). A Ficus was the only tree in which I did not catch a R. gracilis in the tree crown, although one individual was captured on the lower trunk. Traps in all the other trees yielded from 1 to 6 individuals over a 3-day sampling period. On 45% of the trap nights two or more individuals were captured in the same tree on the same night.

Table 2-2. Total number of captures of each species at each height during 2.5 years of trapping on the understory transect.

SPECIES	GROUND CAPTURES	ARBOREAL CAPTURES	N	Chi-square Test*	
				χ^2	P
<u>Heteromys desmarestianus</u>	206	0	206	137.3	<0.0001
<u>Scotinomys teguina</u>	162	0	162	108.0	<0.0001
<u>Oryzomys albigularis</u>	1	0	1	-	-
<u>Oryzomys alfaroi</u>	1	0	1	-	-
<u>Peromyscus nudipes</u>	324	83	407	78.2	<0.0001
<u>Reithrodontomys gracilis</u>	24	260	284	120.3	<0.0001
<u>Nyctomys sumichrasti</u>	0	5	5	-	-
<u>Marmosa mexicana</u>	0	4	4	-	-
			----- 1070		

*df=1, 1:1 expected

Table 2-3. Captures in traps placed in the crowns of canopy trees. Each tree was sampled once for three consecutive days.

TREE SPECIES	HEIGHT TO TRAPS IN CROWN (m)	RODENT SPECIES	NO. OF INDIVIDUALS	NO. OF CAPTURES
<u>Guarea</u> <u>rhopalocarpa</u> (Meliaceae)	13.5	<u>Reithrodontomys gracilis</u>	6	7
<u>Sapium</u> <u>oligoneuron</u> (Euphorbiaceae)	10.5	<u>Reithrodontomys gracilis</u>	4	6
<u>Pouteria</u> sp. (Sapotaceae)	18.5	<u>Nyctomys sumichrasti</u> <u>Reithrodontomys gracilis</u>	1 2	1 2
<u>Bielschmidia</u> <u>mexicana</u> (Lauraceae)	15.0	<u>Reithrodontomys gracilis</u>	3	4
<u>Ficus</u> <u>tuerckheimii</u> (Moraceae)	19.0	<u>Reithrodontomys gracilis</u>	1	1
<u>Meliosma</u> sp. (Sabiaceae)	16.5	<u>Reithrodontomys gracilis</u>	2	2
		-----	19	-----
				23

Despite the number of captures of P. nudipes in the understory vegetation, no individual of this species was captured in the crowns or on the midlevel trunks of trees. To test the possibility that traps placed at the base of the trees prevented P. nudipes from moving past the ground traps and into the higher understory, I removed the ground traps after the first night of trapping. The results remained the same: P. nudipes was never captured at heights above 3 m.

Temporal Consistency in Vertical Distribution Patterns

Circadian patterns in capture. Only one species, the terrestrial Scotinomys teguina, was trapped throughout the day (Figure 2-1). Five of 13 individuals were captured during twilight or nocturnal hours, but of those five, only one was not recaptured during the day. Peromyscus nudipes was also captured during the day, but only three of 34 individuals. With the exception of one individual at 1300 h, captures were made during the few hours between an earlier release at the first morning check and the second check at 0900 h (Figure 2-1). Daytime captures of both species were only in ground traps. Captures of Heteromys desmarestianus (24 captures of 13 individuals) and R. gracilis (25 captures of 11 individuals) were always between 1700 and 0830. Nyctomys sumichrasti was not captured during the session.

Diurnal activity in the canopy by R. gracilis was not assessed in this study. However, other investigators making observations from within the Monteverde canopy in a two month study of bird use of epiphytes (Nadkarni and Matelson, 1989) did not see any mice (T. Matelson, pers. comm.).

Seasonal patterns in capture. Heteromys desmarestianus and S. teguina were taken only in terrestrial traps during the 2.5 year study (Table 2-3) and demonstrated no temporal change in vertical habitat distribution. Nyctomys sumichrasti was uncommon on the transect, but captured only in arboreal traps (Table 2-3). Four of the five captures

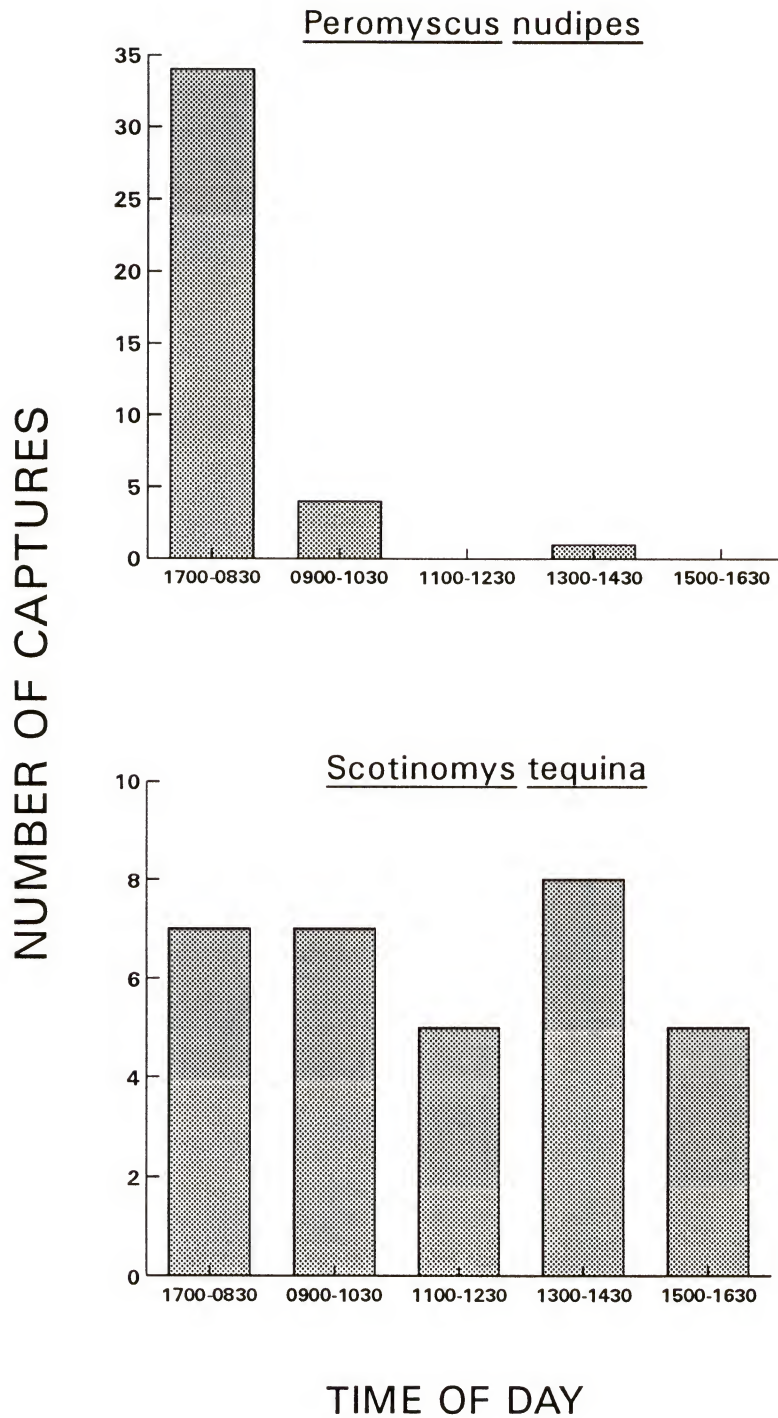


Figure 2-1. Frequencies of diurnal captures of Scotinomys teguina and Peromyscus nudipes on the understory transect, 23-28 March, 1987. Captures of Heteromys desmarestianus and Reithrodontomys gracilis are not presented since all captures were nocturnal. Nyctomys sumichrasti was not captured during this session.

occurred during October and November, 1988, while the fifth capture was not taken until May 1990. The narrow time span over which they were captured may reflect a temporal change in vertical distribution.

Peromyscus nudipes and R. gracilis were captured in both arboreal and terrestrial traps (Table 2-3) and potentially could demonstrate temporal changes in the proportion of captures in each stratum. Plots of captures in arboreal and ground traps at each trapping session showed that proportions fluctuated over time for both species (Figure 2-2). There was no significant correlation for either species between the number of captures in arboreal and ground traps when compared with a Pearson Correlation Coefficient (P. nudipes, $r=0.42$, $P=0.09$; R. gracilis, $r=0.24$, $P=0.35$).

Peromyscus nudipes showed a larger number of arboreal captures in 1987 as compared to the later trapping sessions (Figure 2-2). Reithrodontomys gracilis, in contrast, showed no such pattern and only a slight increase in ground captures in January and February, 1989; generally, ground captures were few and sporadic (Figure 2-2). Tests for differences in the frequency of arboreal and ground captures in the understory between the 1987 and 1988-90 field seasons (Table 2-5) verified these patterns. Peromyscus nudipes demonstrated significant differences between 1987 and 1988-90; 29.9% of its captures in 1987 were in arboreal traps in contrast to only 13.7% in 1988-90. For R. gracilis, the frequencies of capture in arboreal and ground traps were similar between years.

Conceivably, P. nudipes in 1987 could have been influenced by previous trap experience or baited to heights by the close proximity of traps. I tested for this possibility by comparing capture frequencies in 1987 and 1988-90 using data that only included captures in which it was the first time the individual appeared on the transect and at least one trap was open at the adjacent height (Table 2-6). In this case,

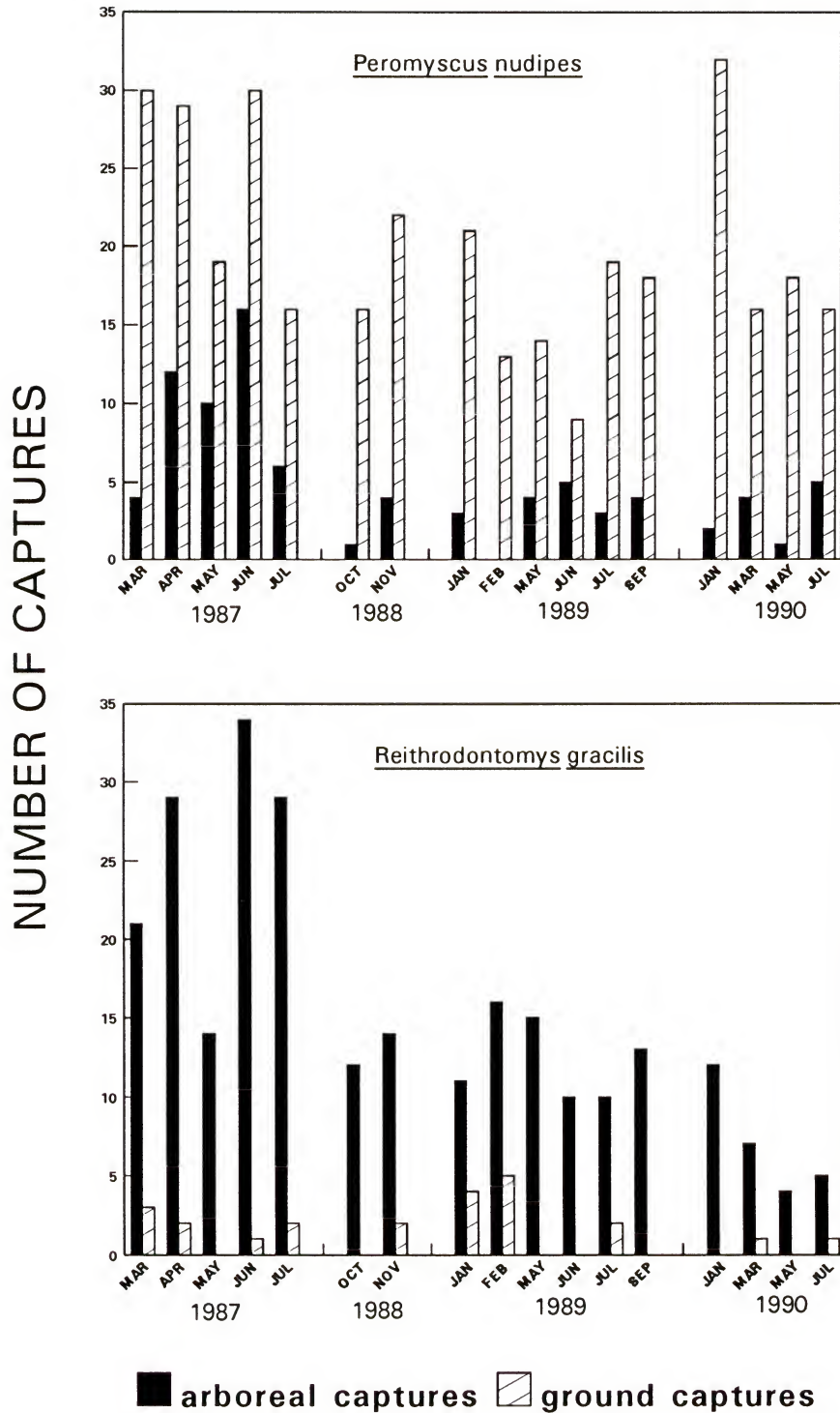


Figure 2-2. Comparison of the number of arboreal and ground captures of Peromyscus nudipes and Reithrodontomys gracilis during each trapping session on the understory transect.

there were no significant differences in capture frequency between 1987 and 1988-90 for either P. nudipes or R. gracilis. Apparently, previous trap experience or baiting heightened the capture of P. nudipes in arboreal traps in 1987.

Table 2-5. Understory capture frequencies based on total number of captures.

	<u>Peromyscus nudipes</u>			<u>Reithrodontomys gracilis</u>		
	<u>ground</u>	<u>arboreal</u>	<u>N</u>	<u>ground</u>	<u>arboreal</u>	<u>N</u>
1987	117 (70.1%)	50 (29.9%)	167	9 (6.4%)	131 (93.6%)	140
1988-90	207 (86.3%)	33 (13.7%)	240	15 (10.4%)	129 (89.6%)	144
Pooled	324 (79.6%)	83 (20.4%)	407	24 (8.5%)	260 (91.5%)	284
	$\chi^2=15.9$, df=1, P<0.0001			$\chi^2=0.227$, df=1, P=0.23		

Table 2-6. Understory capture frequencies based on first capture of an individual and at least one trap open at the adjacent stratum (see text).

	<u>Peromyscus nudipes</u>		<u>Reithrodontomys gracilis</u>	
	<u>ground</u>	<u>arboreal</u>	<u>ground</u>	<u>arboreal</u>
1987	17 (100%)	0	0	14 (100%)
1988-90	59 (92.2%)	5 (7.8%)	5 (10.2%)	44 (89.8%)
Pooled	76 (93.8%)	5 (6.1%)	5 (7.9%)	58 (92.1%)
Fisher's Exact Test	P=0.58		P=0.58	

Additionally, there was no significant difference between years in the proportion of individuals of the population that did not conform to the species-typical distribution pattern (Table 2-7). Individuals captured at heights that contrasted to the species' norm generally were

active in both strata. Those active in only one (10 P. nudipes and 3 R. gracilis) were trapped once or during a single trapping session.

Individuals monitored over several trapping sessions were caught in both arboreal and ground traps. Peromyscus nudipes, however, in contrast to R. gracilis, showed a significantly larger proportion of its population active both on the ground and in the vegetation (Table 2-7, $P=0.02$, $df=1$, $\chi^2=5.378$). Climbing activity was shown by 30.8% of P. nudipes while only 17.6% of R. gracilis showed terrestrial activity during the 2.5 year study.

Table 2-7. Proportion of the population trapped at each height on the understory transect.

<u>Peromyscus nudipes</u>			
	<u>individuals trapped on and off the ground</u>	<u>individuals trapped only on the ground</u>	<u>N</u>
1987	19 (35.8%)	34 (64.2%)	53
1988-90	18 (26.9%)	49 (73.1%)	67
Pooled	37 (30.8%)	83 (69.2%)	120
$\chi^2=1.120$, $df=1$, $P=0.290$			
<u>Reithrodontomys gracilis</u>			
	<u>individuals trapped on and off the ground</u>	<u>individuals trapped only in arboreal traps</u>	<u>N</u>
1987	8 (15.4%)	44 (84.6%)	52
1988-90	11 (19.6%)	45 (80.4%)	56
Pooled	19 (17.6%)	89 (82.4%)	108
$\chi^2=0.337$, $df=1$, $P=0.561$			

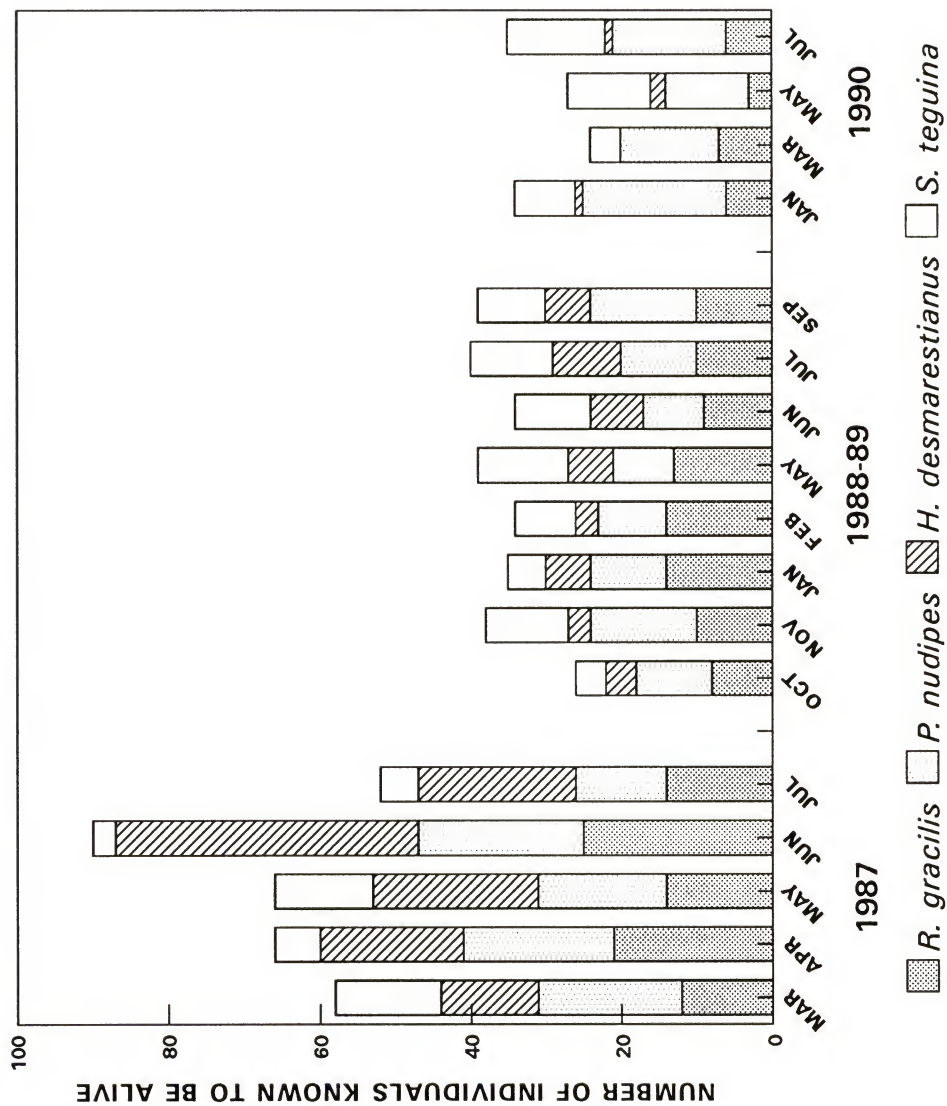


Figure 2-3. The minimum number of individuals known to be alive within the rodent community during each trapping session.

An interesting pattern in population levels within the rodent community was coincident with the larger number of arboreal captures of P. nudipes in 1987. There were more individuals known to be alive on the transect in 1987 than in 1988-90 (Figure 2-3). Peromyscus nudipes showed a significant positive Spearman rank correlation between the number of individuals of all species known to be alive at each session and the proportion of arboreal captures ($r=0.456$, $P<0.05$). However, there was no such correlation for Reithrodontomys gracilis ($r=0.065$, $P>0.05$). The coincident patterns suggest that higher population levels, particularly on the forest floor, may have influenced some individuals of P. nudipes to spend more time in the lower understory.

Discussion

Vertical Distribution Patterns

The results of the trapping study indicate that the five most common species of mice in Campbell's Woods are vertically stratified in the forest (Figure 2-4; Table 2-8). The vertical distribution patterns are consistent with patterns described by other investigators, but provide more detail since three-dimensional trapping schemes, particularly in the crowns of canopy trees, have not been employed in previous studies. Populations of S. teguina (Hooper and Carleton, 1976) and H. desmarestianus (Fleming, 1974a) at other sites in Costa Rica also demonstrated terrestrial activity. The extremely arboreal nature of N. sumichrasti has been reported by numerous mammalogists (Ceballos, 1990; Goodwin, 1946; Genoways and Jones, 1972). Limited climbing by P. nudipes has been reported (Lumer, 1980; McPherson, 1985), but a terrestrial designation is generally assigned to this species (Anderson, 1982; Timm et al., 1989). Reithrodontomys gracilis was reported by Young and Jones (1984) as only "somewhat scansorial" and nowhere common. Genoways and Jones (1972), based on visual observations, reported that a

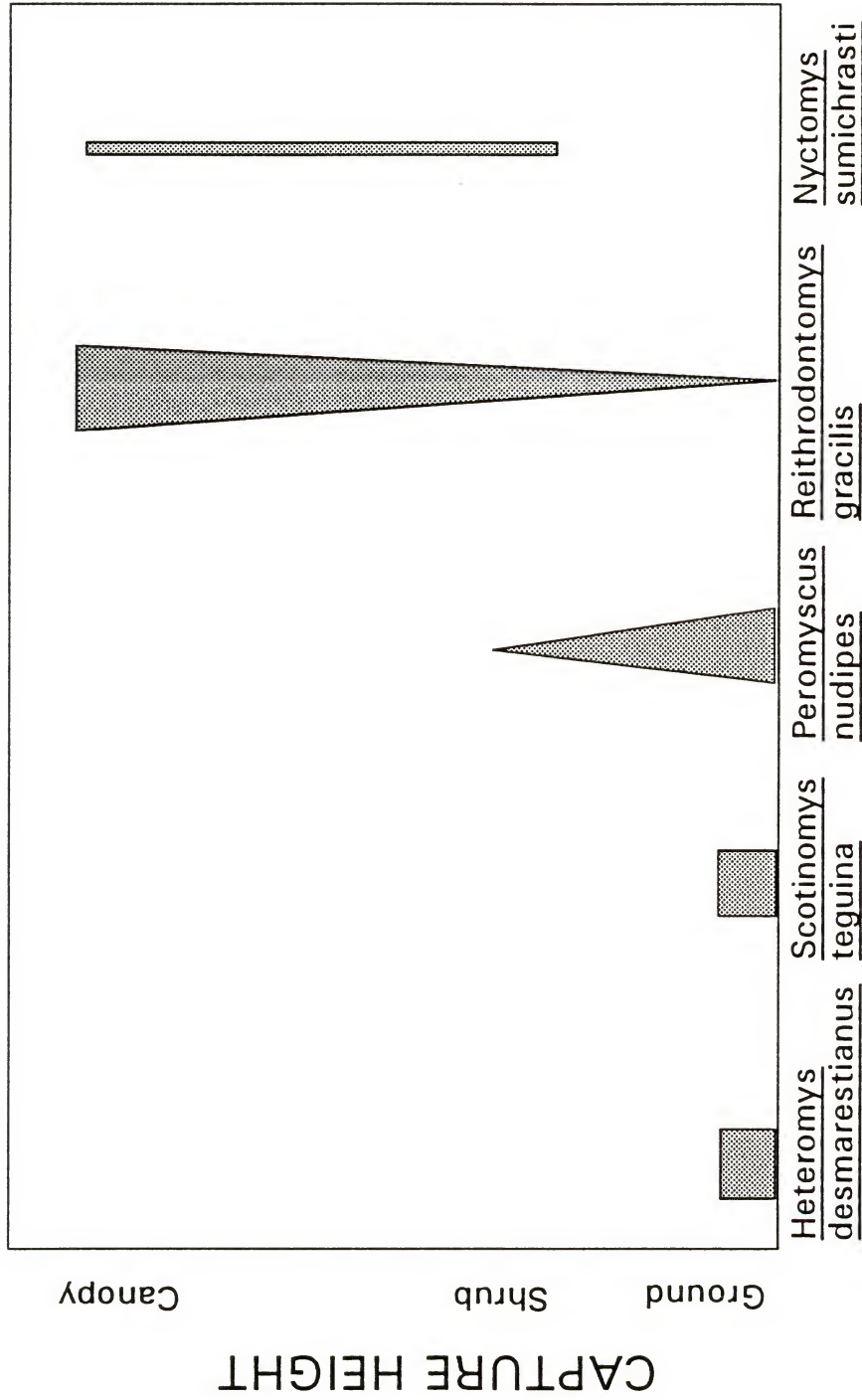


Figure 2-4. Diagrammatic representation of the vertical distribution of the five most common species of mice in Campbell's Woods. Narrowing of the bars represents an inferred lower frequency of occurrence within the stratum relative to other strata or other species.

Table 2-8. Summary chart of the distribution and behavior patterns described by the results of the trapping study.

SPECIES	DISTRIBUTION	HABITAT PREFERENCE	VARIATION AMONG INDIVIDUALS	FACULTATIVE CHANGES OVER TIME	SPECIALIZATION
<u>Scotinomys</u> <u>teguina</u>	forest floor	forest floor	no	no	specialized terrestrial
<u>Heteromys</u> <u>desmarestianus</u>	forest floor	forest floor	no	no	specialized terrestrial
<u>Peromyscus</u> <u>nudipes</u>	forest floor understory	forest floor	yes	yes	generalized terrestrial
<u>Reithrodontomys</u> <u>gracilis</u>	forest floor understory crowns	understory crowns	yes	no	generalized arboreal
<u>Nyctomys</u> <u>sumichrasti</u>	understory crowns	crowns	?	yes?	specialized arboreal

population in Nicaragua inhabited only the forest floor and lowest strata of a riparian forest. The abundance of individuals 1 to 13.5 m above the forest floor in Monteverde suggests that climbing activity may vary widely among populations and that much more sampling high in the habitat is required to define adequately the distribution and abundance of the populations of this species.

Fidelity to a Particular Stratum

Heteromys desmarestianus and S. tequina showed no variation in capture patterns and appear to have a strong preference and fidelity to the forest floor (Table 2-8). The population of P. nudipes at Monteverde, although predominantly found on the forest floor, contained individuals that frequented both strata. Although the proportion of the population that climbed did not change from 1987 to 1988-90, the proportion of arboreal captures did, with apparent association to an individual's previous experience in a ground trap and to increased population levels. The trapping results suggest a preference for, but not a strong fidelity to, the forest floor. In contrast, R. gracilis predominantly frequented arboreal habitats, but some individuals also frequented the forest floor. The proportion of the population that showed behavior in contrast to the species' norm, however, was less than that of P. nudipes. There were also no associations between terrestrial captures of R. gracilis and previous trap experience, baiting, or changes in population levels.

Fidelity to a vertical stratum by N. sumichrasti is not clear from my few captures. However, similar to the seasonal clumping of understory captures in this study, Fleming (1970) documented the sudden appearance and disappearance of N. sumichrasti in traps set on the ground and in understory plants during and after a six-month period of reduced tree fruiting in Panama. Fleming proposed that a scarcity of food drew the animals to lower strata of the forest where they do not

normally forage. The capture pattern on my site may also indicate a vertical shift in foraging behavior for the species due to scarce resources; however, detailed monitoring of the population and fruiting patterns in the canopy and understory is required to test the hypothesis.

The Adaptiveness of Stratum Fidelity

Fidelity to a certain stratum in the forest, as apparently is the case for H. desmarestianus, S. tequina, and N. sumichrasti, can be adaptive to individuals if it leads to increased efficiency in the use of resources at that level with a concomitant increase in fitness. Relaxed fidelity, such as the variation and plasticity in habitat use evident in P. nudipes and R. gracilis, can also be adaptive if, by partitioning foraging time between the forest floor and understory/canopy plants, individuals ameliorate the adverse effects of scarce resources or competition from heterospecifics or conspecifics (Futuyma and Moreno, 1988). This may account for the correlation between the change in arboreal captures of P. nudipes and the change in population levels between 1987 and 1988-90. Arboreal captures could have increased as a result of higher levels of intra- or interspecific competition for food or other resources, and/or there may have been a coincident change in resource abundance on the ground, independent of population levels, that drew individuals to arboreal traps.

The effects of previous trap experience and baiting on arboreal captures of P. nudipes in 1987 suggest a possible adaptive advantage. Based on the analyses that controlled for previous experience and baiting, it appears that individuals normally foraged on the ground. However, once an animal encountered a trap and recognized it as a source of food, it was more likely to enter arboreal traps. Loose bait on the ground and odor emanating from the traps may be cues that drew the animals to the arboreal traps. A comparable situation in the wild may

exist as fruit begins to ripen in understory plants and falls to the forest floor. Individuals may learn to recognize potential food sources from chance discoveries on the forest floor and then climb to harvest the remaining crop, giving them an advantage over scavenging non-climbing competitors. This hypothesis could be tested with captive individuals.

Relaxed fidelity can also be adaptive if it contributes to the ability of individuals to survive and adapt to long-term changes in the habitat or to disperse into new habitats when existing conditions are detrimental to fitness. The variation evident in P. nudipes and R. gracilis indicates not only a behavioral flexibility to cope with short-term changes, but a potential to respond to natural selection imposed by long-term changes (Futuyma and Moreno, 1988). Temporally unstable environments will generate selection for genotypes that select habitats under-used by competitors and thus maintain variation in the population either in the form of polymorphisms or individual behavioral flexibility. A change to a different, but temporally stable environment, could drive the population to specialize in either the arboreal or terrestrial habitat, depending on which strategy produces the greatest individual fitness.

The nature of the individual variation in climbing behavior in the P. nudipes and R. gracilis populations during the trapping study requires further study. It is unknown if all individuals in each population frequent both strata and trapping did not detect this, or if the variation is real and only a few individuals are active in both strata. The apparent variation could be due to chance or differences among individuals in either previous experience or genotype.

Stratum Fidelity and Habitat Specialization

The results of the trapping study support the use of temporal changes in the proportion of a population captured in ground and

arboreal traps as a quantitative measure of behavioral fidelity to a particular stratum and as a character for further studies of adaptive value. The species-typical nature of the character and the apparent correlation of character states with vertical specialization as described by distribution patterns make stratum fidelity a strong candidate for comparative study of the evolution of vertical specialization. Explanations as to the function of the behavior and fitness differences expected of variants are plausible and could be tested in comparative studies. The character, however, as described in this study, appears to represent a complex set of features that may be more appropriately analyzed if reduced to more discrete components. The expression of the character under the influence of learning and previous experience as well as specific ecological factors in the habitat (such as inter- and intraspecific competition and changes in resource levels) is unknown and needs to be assessed. Additional behavioral characters may underlie fidelity patterns as well, and in the following chapter I examine one of these.

CHAPTER 3 ESCAPE RESPONSE AND CLIMBING DISPOSITION

Introduction

The vertical distribution patterns of the mice in Monteverde result from the climbing behavior of individuals while foraging, reproducing, nesting, or avoiding predation. The species-typical nature of the patterns suggests that individuals of each population share a common "set of rules" that determine when, where, and under what conditions they climb. The use of behavioral rules in choosing a vertical stratum is an important component in habitat specialization, because the consequences of climbing decisions can either increase or decrease survival and reproductive success (see discussion in Chapter 2 and Real, 1991).

One particular feature of climbing behavior that can provide a strong basis for decision-making is climbing disposition, or the psychological inclination to climb. Experimental studies of captive-reared species of mice have demonstrated the species-typical nature of this behavior and its correlation with vertical activity of the wild parent stock (Birkenholz and Wirth, 1965; Crozier and Pincus, 1926a; 1933; Dewsbury et al., 1980; Horner, 1954; Layne, 1970; Thompson, 1990). A strong disposition for, or a strong disposition against climbing, could enhance ecological specialization in a particular vertical stratum, while ambivalence in climbing could promote behavioral plasticity and the generalized use of several strata. Nevertheless, biotic and abiotic factors in the environment, as well as climbing ability and locomotor morphology, can also influence climbing decisions, and this raises two important questions: 1) How does climbing

disposition differ among species that inhabit different vertical strata and vary in their degree of fidelity? 2) What is the relative contribution of climbing disposition to specialization; is it strong enough to override the influence of other factors? Answers can give insight into the perceptual rules individuals of a population employ in habitat selection, and the consequences these hold for ecological interactions and the evolution of ecological specialization.

A major impediment to such an investigation, however, is the difficulty of quantifying climbing disposition independent of the other factors that influence climbing behavior. Many environmental factors can be controlled and/or tested in captive experiments, but differentiating between climbing disposition and climbing ability is particularly difficult because the two act in conjunction to describe climbing performance, the most easily measured variable in climbing experiments. Captive studies of various species of mice (Horner, 1954; Layne, 1970; Dewsbury et al., 1980) and Anolis lizards (Pounds, 1988) have demonstrated the importance of both features in climbing performance.

I took a different approach to the problem and designed a series of choice experiments in which the behavioral rules expected to operate in decisions based on climbing disposition were opposed to the behavioral rules expected to operate if climbing morphology, and hence climbing ability, were the basis for decisions. In the manner of behavioral titration, individuals were forced to choose between the two, indicating priority or a hierarchy in the use of these sets of decision-making rules (Real, 1991). This conflict approach was first advocated by Crozier and Pincus (1926a; 1926b; 1933) in a series of experiments analyzing the contributions of different types of tropisms to behavior in young rats. I conducted the experiments in the field in association with the trapping study, which also allowed me to look for possible effects from natural temporal variation within the habitat (i.e.,

season, weather conditions, population levels; See Chapters 1 and 2). The semi-natural conditions also avoided some of the confounding effects from confinement identified in previous captive experiments (Henderson, 1970; Layne 1969; 1970; Layne and Ehrhart, 1970).

I focussed on the escape responses of individuals and whether or not they chose to climb when I released them at their site of capture. I first established the preference of each population to climb when escaping, without attempting to differentiate between climbing disposition and climbing ability. I then tested the relative strength of that preference in a separate experiment in which I presented individuals with a choice between an escape route that was easy to climb but led to the stratum they did not prefer, and an escape route that was more difficult to climb but led to the preferred stratum. If disposition dominated the decision-making process, individuals should seek a preferred vertical stratum regardless of climbing difficulty; if locomotor ability dominated, individuals should be more sensitive to the difficulty of climbing the substrate and choose the easier route of escape.

Rationale for the Experimental Design

I chose escape response as an index of climbing disposition based on the assumption that individuals would react to my presence as a possible predator and spontaneously seek the stratum for which they were best adapted (Williams, 1966). Since my behavior while trapping and handling the animals was out of the range of normal experiences the mice usually encountered with natural predators, I assumed they would demonstrate their natural climbing disposition rather than an evolved response to a specific type of predator.

I assumed the climbing rules based on climbing disposition and climbing ability would differ because disposition and ability are each a property of a different organ system of the body that detects and

responds to different environmental stimuli. Climbing ability is predominantly a property of locomotor morphology. Biomechanic studies have shown that climbing performance based on ability is dependent on morphology and sensitive to physical attributes of the climbing substrate such as branch diameter, flexibility, and inclination (Badoux, 1974; Cartmill, 1974; 1985; Horner, 1954; Pounds, 1988). Climbing disposition, in contrast, is predominantly a property of the nervous system and endocrine system, a psychological response to the environment from the brain after signals have been sensed, integrated, perceived, and interpreted (King, 1968). Behaviorists and comparative psychologists have shown that climbing individuals react not only to the structure of the climbing substrate, but also to gravity (Crozier and Pincus, 1926a; 1933; Birkenholz and Wirth, 1965), height above ground (Horner, 1954), perceived edges or vertical cliffs (Horner, 1954; Sloane et al., 1978), and the presence of light (Crozier and Pincus, 1926b; Fitzgerald and Wolff, 1988).

To establish the preferred direction of escape, I quantified the response of individuals released on the ground, as well as on a standardized arboreal substrate that mimicked natural vegetation. The climbing substrate, called a vertical T-maze, presented the animals with two directions of escape at a T-intersection, one a climb (or jump) down to the forest floor and the other a climb up into arboreal vegetation (Figure 3-1, described in detail in materials and methods). I carried the T-maze with me as I checked the traps and ran the experiments immediately after recording data for each animal. The semi-artificial substrate allowed me to standardize climbing conditions in order to compare choices among and within species.

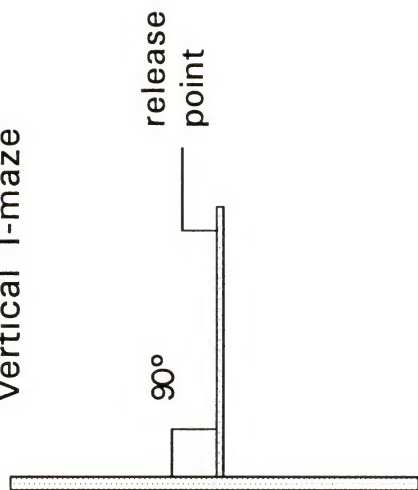
To differentiate climbing disposition from climbing ability, I modified the design of the T-maze experiment such that there was an increase in climbing difficulty of the original preferred route of escape; thus, climbing disposition would be in conflict with climbing

ability. To increase climbing difficulty, I changed the angle of inclination encountered by the individual at the T-intersection. The apparatus approximated a Y-maze presenting acute or obtuse angles of inclination to the escaping mouse (Figure 3-1).

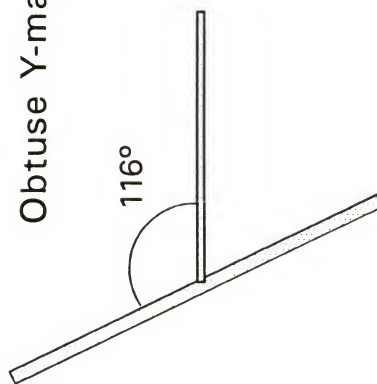
Studies of the biomechanics of locomotion in climbing primates (Badoux, 1974; Cartmill, 1972) and mammals such as squirrels and marsupials (Cartmill, 1974) have demonstrated that the angle of inclination of a branch affects the degree of climbing difficulty (see Cartmill, 1985 for a review). Animals climbing on an inclined surface must contend with the force of gravity. When an animal stands on a horizontal support, there is a reaction force from the substrate that is in direct opposition to the force of gravity acting on the mass of the animal. The animal is only in danger of slipping sideways off the support and needs only to maintain its balance. As the angle of inclination increases, the force of gravity is no longer perpendicular to the substrate, but oblique, and the animal is in danger of slipping down the support. When the branch is vertical, no force is provided by the substrate to counteract gravity, and specialized behavior and morphologies (Chapter 1) that enhance frictional forces between the animal and the support must be used to prevent falling (Cartmill, 1974; 1985; Thorington and Thorington, 1989).

By changing the angle of encounter and branch inclination of the T-maze away from vertical (Figure 3-1), the individual at the T-intersection was presented with a choice of two escape routes that required different motor skills. With an escape along the arm that followed the obtuse, the substrate was always beneath the animal, providing support against the force of gravity (Cartmill, 1974; 1985). With a choice in the opposite direction, along the arm that followed the acute angle, the same gentle slope was encountered, but the animal faced a maneuver at the intersection that required it to climb into position on the escape arm, at which point, the substrate was vertical and no

Vertical T-maze



Obtuse Y-maze



Acute Y-maze

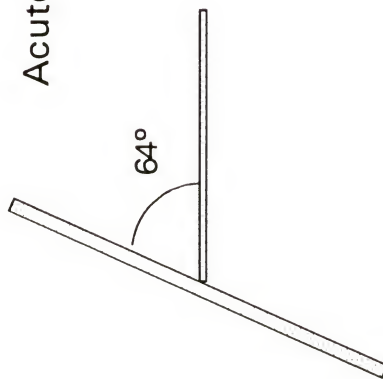


Figure 3-1. Apparatus used to test climbing escape response. A mouse escaping along the horizontal arm of the vertical T-maze encountered a 90° angle at the intersection of the maze and a vertical climb up or down. The obtuse Y-maze presented an obtuse angle to the mouse and an easier climb up than down. The acute Y-maze presented an acute angle to an escaping mouse and an easier climb down than up (see text).

longer countering gravity. Escape along the arm of the obtuse angle should be more expeditious than escape along the acute angle for three reasons: 1) balance on the substrate was the major motor skill required on the obtuse arm, and is a general skill that functions in terrestrial as well as arboreal locomotion, 2) a time-consuming positional maneuver is not required at the intersection, and 3) energy is not expended while clinging to the support to gain position. I expected both the terrestrial and arboreal species to choose the obtuse arm for escape if efficiency of locomotion, rather than psychological disposition, was the major factor influencing escape decisions.

Materials and Methods

After processing captured animals for trapping data, I released individuals at their site of capture onto the climbing substrates. Animals were placed in a cloth bag and allowed to work their way free. Behavioral choices were recorded, and frequencies were compared using a Chi-square test or, when sample sizes were small, Fisher Exact Probability tests using SAS (SAS Institute Inc., 1987). Species-typical preferences in escape choice were examined by testing frequencies against a null model of 1:1 expected.

In the first experiment, I released the animal on the ground in the middle of the trail. I observed the animal's progress as far as possible and recorded its decision to climb or not to climb. I discarded from the analysis trials in which I could only follow the animal for less than 2 m. If an individual was subsequently recaptured, I repeated the procedure, but analyzed repeated trials separate from first trials. Individuals were represented only once in each analysis so as not to violate the assumption of independence of the Chi-square test. To obtain an adequate sample of individuals, I conducted the experiment during trapping sessions that spanned several months. The experiment was first conducted in June and July, 1987, when population

levels were high, and repeated the next field season in 1989, when population numbers were lower (Chapter 2).

In the second experiment, I released individuals on the vertical T-maze. The T-maze was cut from a shrub and consisted of a vertical branch approximately 2 m long and 25 mm thick. At its midpoint a horizontal arm came off the vertical at a 90° angle, dividing the vertical arm into two equal parts at a T-intersection (Figure 3-1). The apparatus was positioned such that one end of the vertical arm rested on the ground while the other end rested on a branch of an overhanging tree or shrub. I took care to make sure the apparatus was clear of vegetation along its length so that a mouse could not leap to any other climbing substrates before reaching the ground or overhanging branch. Between trials I rotated the T-maze 180° on its horizontal axis and rubbed the arms with the urine tainted handling bag to confound a mouse using olfactory cues to choose a path of escape.

I placed the cloth bag containing the mouse on the horizontal arm with the bag opening facing the T-intersection and positioned the mouse until I could feel that it was resting quietly on the horizontal arm. Supporting the arm of the apparatus with one hand, I removed my other hand from the bag opening and allowed the mouse to work its way free. The animal faced two choices as it escaped from the bag: (a) run along the horizontal arm or (b) jump down. If it ran along the arm, it then faced another set of choices at the T-intersection: (a) climb up the vertical arm to the overhanging branch, (b) climb down to the forest floor, or (c) jump down. The experiment was run initially in June and July, 1987 and repeated in 1989.

On three occasions in 1989, I conducted the trials before dawn under twilight and nocturnal light levels to test for the possibility of different escape responses to predators active at those times, or to variations in light intensities that could affect vision and navigation. I used a headlamp covered with a red filter to observe the responses.

Dim red light is commonly used in zoos, laboratories, and the field to observe the behavior of nocturnal animals on the assumption that mammals with predominantly rod vision are not sensitive to red wavelengths of low intensity (Finley, 1959; but see Vestal and Hill, 1972). Only P. nudipes and R. gracilis were tested, as individuals of H. desmarestianus were rare that year, and S. tequima was predominantly diurnal and not captured.

In the third experiment, I released a new set of individuals on the angled Y-maze. The Y-maze was cut from the same shrub as the T-maze. In each trial, I oriented the Y-maze such that the expected arm of escape was in opposition to the climbing disposition demonstrated by trapping and previous escape experiments, and tested for consistency in species-typical climbing decisions between the two experiments. Because there were not adequate numbers of individuals to test each species on both the acute and obtuse Y-maze, for those species that showed a strong disposition to climb up on the vertical apparatus, I used a Y-maze that presented an acute angle of ascent (64°) from the horizontal (Fig 3-1, acute Y-maze). For those species that showed a strong disposition to climb down or jump down, I rotated the Y-maze 180° such that an obtuse angle (116°) was encountered by individuals at the intersection (Fig 3-1, obtuse Y-maze). I took particular care to rub the entire apparatus with the urine tainted handling bag between trials in order to reduce the possibility of an individual following a scent trail, since I could not rotate the Y-maze and maintain the appropriate test angle.

I followed the same protocol as in the vertical T-maze experiment. Heteromys desmarestianus was not tested in the final experiment because of the small number of individuals found on the transect at that time.

Results

Releases on the Ground

Individual decisions to climb when released on the ground were consistent within species and corresponded with the climbing habit revealed by the trapping study. Reithrodontomys gracilis, which was captured predominantly in arboreal traps, was the only species observed to climb into the vegetation spontaneously when released on the ground; individuals did so more than half the time (Table 3-1). There were no significant differences in climbing choice between the sexes ($\chi^2=0.019$, $df=1$, $P=.89$) nor between the 1987 and 1989 field seasons ($\chi^2=0.011$, $P=0.917$). Individuals that climbed used small-diameter saplings, branchlets, and vines for escape. I observed individuals that climbed 20 to 30 m into the canopy along vines and lianas, as well as individuals that moved horizontally through the forest understory, remaining 1 to 4 m off the forest floor, leaping between branches and plants. This behavior was observed in windy, calm, wet, and dry weather.

Table 3-1 Escape choices of individuals released on the ground.

SPECIES	N	REMAIN ON GROUND	CLIMB UP	VERTICAL HABIT*
<u>Heteromys desmarestianus</u>	33	33 (100%)	0	terrestrial
<u>Scotinomys teguina</u>	34	34 (100%)	0	terrestrial
<u>Peromyscus nudipes</u>	59	59 (100%)	0	scansorial
<u>Reithrodontomys gracilis</u>	50	21 (42%)	29 (58%)	arboreal

* based on results of the trapping study

Peromyscus nudipes, sometimes trapped in the vegetation, never climbed into the understory after release on the ground. It did,

however, climb along surface roots or downed limbs and branches before disappearing in the undergrowth. Anderson (1982) described similar behavior for the species during his earlier research in Monteverde. Heteromys desmarestianus and S. tequina never climbed and ran under cover or into holes.

Releases on the Vertical T-maze

Individuals released on the horizontal arm of the vertical T-maze also demonstrated species-typical escape responses (Table 3-2). The two climbing species, P. nudipes and R. gracilis, were equally likely to run along the horizontal arm as to jump from the apparatus. The two terrestrial species, however, showed statistically significant tendencies for one type of escape response: the majority of the S. tequina ran the horizontal arm, whereas the majority of the H. desmarestianus jumped from the apparatus before reaching the T-intersection. Four H. desmarestianus fell rather than jumped off the horizontal arm.

Table 3-2. Escape choices on horizontal arm of the vertical T-maze.

SPECIES	N	TRAVERSE ARM	JUMP DOWN	VERTICAL HABIT*
<u>Heteromys desmarestianus</u>	44	12 (27.3%)	32 ** (72.7%)	terrestrial
<u>Scotinomys tequina</u>	31	25 (80.6%)	6 ** (19.4%)	terrestrial
<u>Peromyscus nudipes</u>	41	25 (61.0%)	16 (39.0%)	scansorial
<u>Reithrodontomys gracilis</u>	35	22 (62.9%)	13 (37.1%)	arboreal

* based on results of trapping study

** df=1, 1:1 expected, P<0.03

At the T-intersection of the vertical T-maze, choices of individuals were species-typical with little variation among individuals (Table 3-3). I pooled the data for each species for the 1987 and 1989

trials, as no differences were found between years, despite the fact that individuals in 1987 were marked by one to two clipped toes. The two climbing species that displayed similar behaviors on the horizontal arm diverged in their choices at the T-intersection. The scansorial P. nudipes climbed down, while the arboreal R. gracilis climbed up. Heteromys desmarestianus always jumped down, similar to its behavior on the horizontal arm. Scotinomys tequima was equally likely to climb down or to jump down from the apparatus.

Table 3-3. Escape choice at the T-intersection of the vertical T-maze.

SPECIES	N	CLIMB UP	CLIMB DOWN	JUMP DOWN	VERTICAL HABIT*
<u>Heteromys desmarestianus</u>	12	0	0	12 (100%)	terrestrial
<u>Scotinomys tequima</u>	25	1 (4.0%)	12 (48.0%)	12 (48.0%)	terrestrial
<u>Peromyscus nudipes</u>	25	0	21 (84.0%)	4 (16.0%)	scansorial
<u>Reithrodontomys gracilis</u>	22	21 (95.5%)	1 (4.5%)	0	arboreal

* based on the results of the trapping study

Repeated tests of individuals after subsequent recapture failed to show differences in choices as a result of previous experience on the apparatus. Ten R. gracilis were tested twice, and two were tested three times. Only one individual climbed down at the T-intersection. This female jumped down and again climbed down during two more trials. Of the 41 P. nudipes tested, 17 were tested a second time, and 6 a third time. Only one individual climbed up in repeated trials. This male jumped down initially, climbed up in the second trial, only to climb down the third time. Twelve repeated tests of S. tequima failed to reveal additional individuals that chose to climb up. The one individual that climbed up in the first trial, a male, jumped down before reaching the T-intersection in a second trial. Ten individuals

of H. desmarestianus were retested and showed no differences from decisions made in the first trial. Two individuals that negotiated the horizontal arm in the first trial fell in a second trial.

Choices made by individuals released in the dark were comparable. I tested nine R. gracilis and six P. nudipes. None of the individuals jumped from the apparatus. All of the P. nudipes climbed down at the T-intersection. Seven of the nine R. gracilis climbed up, while the other two climbed down. When handling and releasing the animals, I noticed no qualitative differences in temperament or behavior from those released in daylight.

Releases on the Angled Y-maze

In contrast to the consistent decisions made by individuals of a species at the T-intersection of the vertical T-maze, the choices made on the angled Y-maze were quite different (Table 3-4). Changing the angle of inclination induced a different species-typical escape response at the T-intersection and introduced greater variation among individuals in climbing decisions.

Table 3-4. Comparison of escape choices on the T-maze and the Y-maze.

SPECIES	N	ANGLE OF ENCOUNTER	CLIMB UP	CLIMB DOWN	JUMP DOWN	FISHER'S EXACT TEST
<u>Scotinomys</u>	22	vertical	1	12	9	P=0.368
<u>tequina</u>	13	obtuse	3	6	4	
<u>Peromyscus</u>	20	vertical	0	17	3	P=0.000004
<u>nudipes</u>	21	obtuse	14	5	2	
<u>Reithrodontomys</u>	18	vertical	17	1	0	P=0.0005
<u>gracilis</u>	14	acute	5	9	0	

The differences in escape choice between the vertical and angled substrates were most pronounced for R. gracilis and P. nudipes. Whereas individuals of P. nudipes invariably climbed down on the vertical T-maze, choices on the angled Y-maze varied and included escape by

climbing, a behavior not exhibited by the species in the previous experiments. With an easy ascent, 65% of the P. nudipes climbed up. Reithrodontomys gracilis also showed significant differences between the two experiments in the proportion of individuals that climbed. While 36% of the individuals climbed up, more individuals climbed down when presented with an acute angle of ascent. In sharp contrast, the terrestrial S. tequina did not show significant differences in escape response between the two experiments. Most individuals chose to climb down or jump down on both the T-maze and Y-maze. Although the number of individuals that climbed up increased to 23% on the Y-maze, the difference was not significant (Table 3-4).

Of those individuals of P. nudipes that followed the easier incline on the angled Y-maze and climbed up, five reversed direction midway up the obtuse arm and climbed down; three stopped after climbing into the natural vegetation and then climbed down when I removed the apparatus. All three of the S. tequina that climbed up, also stopped midway up the obtuse arm and then jumped from the apparatus. I observed four out of nine individuals of R. gracilis spontaneously climb back into the vegetation after they climbed to the ground. For all three species, the choices made by the sexes on the angled Y-maze did not differ significantly (Fisher's Exact Probability Test, $P > .49$).

Peromyscus nudipes was the only species with adequate recaptures to test individuals in repeated trials. Previous experience on the apparatus may have influenced decisions during a second test on the Y-maze. Five of 11 individuals who climbed up or jumped down initially, chose to climb down when the trial was repeated.

Nyctomys sumichrasti, an arboreal species, was not tested on the escape apparatus because it was not commonly trapped on the understory transect. The five individuals captured, however, climbed into the vegetation when released. Climbing was also the escape response when I released into the wild two subadults born and raised in captivity. With

no climbing experience outside of a hardware cloth cage, both immediately climbed trees. One was lost from sight after it climbed over 13 m up the trunk of a canopy tree.

Discussion

Escape Response and Vertical Distribution Patterns

The escape choices that individuals made as I released them on the ground, on the vertical T-maze, and on the angled Y-maze were species-typical and corresponded with climbing behavior expected of individuals that showed the vertical distribution patterns identified in the trapping study (Table 3-5). Terrestrial and scansorial species escaped to the forest floor, whereas the arboreal species escaped to the trees when released on the ground and on the vertical T-maze. In addition, the scansorial nature of *P. nudipes* was evident in the results of the angled Y-maze experiment. Although it climbed only occasionally in the trapping study and showed a preference for terrestrial escapes in the first sets of experiments, climbing decisions on the Y-maze were predominantly influenced by expediency of locomotion and sensitivity to the structure of the substrate rather than by a preference for the forest floor.

Escape Response as an Index of Climbing Disposition

Several features in the response of the animals to the experimental conditions suggest that the escape behavior measured in the study reflects not only an evasive response to a potential predator but also a psychological disposition to climb. The behavior of individuals while negotiating the two mazes was particularly revealing. Upon exiting the cloth bag and at the T-intersection, animals often paused, and, before making a move in a given direction, scanned the surroundings. Their vibrissae twitched repeatedly and the head moved back and forth between the escape routes. Some individuals began to

Table 3-5. Summary chart of the results of the escape response experiments (Chapter 3).

SPECIES	VERTICAL SPECIALIZATION	ESCAPE ON GROUND RELEASE	ESCAPE ON HORIZONTAL ARM	ESCAPE AT ON VERTICAL T-MAZE	ESCAPE ON ANGLED Y-MAZE
<u>Scotinomys</u> <u>tequima</u>	terrestrial	forest floor	run	climb down	climb down
<u>Heteromys</u> <u>desmarestianus</u>	terrestrial	forest floor	jump	jump down	?
<u>Peromyscus</u> <u>nudipes</u>	scansorial	forest floor	run/jump	climb down	climb up
<u>Reithrodontomys</u> <u>gracilis</u>	arboreal	forest floor understory	run/jump	climb up	climb down
<u>Nyctomys</u> <u>sumichrasti</u>	arboreal	understory	?	?	?

move in one direction and then stopped and moved in the other direction. It appeared that the animals were assessing the environment and their options and then making a decision. Since I did not chase the animals along the apparatus, some individuals would pause for several seconds before making an escape choice. Some individuals of all species (excluding R. gracilis) would double back toward me after stopping at the T-intersection. All of this suggests that the threat of predation may not have been the primary factor influencing the behavioral response, and the choices made truly reflect climbing disposition.

Furthermore, all of the species tested showed much greater variation in choices among individuals on the angled Y-maze than on the vertical T-maze (Table 3-4). This variation may have resulted from the conflict generated by the abnormal opposition of 1) a species-typical response to the difficulty of the climbing substrate, with 2) a species-typical preference for one stratum.

Climbing Disposition and Decision-making Rules in Habitat Choice

The relative strength of the influence of climbing disposition on climbing decisions became apparent when individuals were forced to choose between a preferred vertical stratum and an easier escape route. For S. tequina, climbing disposition took precedence over ease of locomotion, while the reverse was true for the climbing species. The scansorial P. nudipes, however, in contrast to the arboreal R. gracilis, showed less variation among the members of its population and consistently chose the easier escape route, regardless of stratum preference; climbing disposition may have had a stronger influence on the behavioral decisions of R. gracilis than on P. nudipes.

Climbing disposition was consistent over time and did not change with factors in the environment. There were no differences in the escape response of species between seasons or years, and species-typical choices did not vary with changes in population numbers. The

experimental trials were conducted under wet, dry, windy, and calm conditions with no apparent effect. Individuals marked with a clipped toe in 1987 made the same species-typical choices as individuals marked with an ear tag or an ear notch the following field season. This consistency suggests that climbing disposition may be less influenced by environmental factors, learning, or experience, than behavioral fidelity to a vertical stratum. The strong climbing response of the two naive captive-born individuals of *N. sumichrasti* after release into the wild further supports this. Experiments with captive-reared individuals are needed to discern the role of learning.

The results of the experiments also suggest that climbing disposition makes a strong contribution to the decision-making process of habitat selection. A similar psychological disposition for specific types of habitat and its role in habitat selection has been documented for several species of birds (Greenberg 1983, 1990) and for populations of terrestrial mice (Harris, 1952; Wecker, 1963). The differences among the species of this study in their response to the conflicting conditions presented in the angled Y-maze experiment further suggest that there may be species-typical differences in the precedence or hierarchy of sets of decision-making "rules". If this is true, observed patterns of vertical specialization may be due to interspecific differences in a psychological disposition for one stratum over others and the ability of environmental factors to over-rule that disposition.

Other sets of decision-making rules involved in habitat selection, in addition to a psychological disposition (Greenberg, 1983; 1990; Harris, 1952; Wecker, 1963; this study) and the biomechanics of locomotion (Horner, 1954; Pounds, 1988; Smartt, 1978), also have been identified and the implications for survival and reproductive success have been demonstrated. These include density-dependent habitat selection and the ideal free distribution (Fretwell and Lucas, 1970; Morris, 1989), energetics and optimal foraging theory (Krebs, 1978;

Real, 1991), and the physiological (for example, osmotic and thermoregulative) consequences of habitat selection (Huey, 1991). All are important to fitness, and selection will act to define not only each set of decision rules, but also the computational rules that establish the precedence or hierarchy of each set of rules in the overall decision-making process (Real, 1991). Differences among species in the hierarchy of rules imply important consequences for observed patterns in community structure, the response of species to short- and long-term changes in the habitat, and the evolution of adaptations associated with habitat specialization.

Climbing Disposition and Vertical Habitat Specialization

The results of the escape experiments support the use of escape response as a quantitative measure of climbing disposition and as a character for further studies of adaptive value. The species-typical nature of the character and the apparent correlation of character states with habitat fidelity and vertical distribution patterns make it a strong candidate for comparative study of the evolution of vertical specialization. Similar to stratum fidelity, explanations as to adaptive functions of climbing disposition and fitness differences expected of variants are plausible and could be tested in comparative studies. However, climbing disposition may be more amenable to phylogenetic analysis in the evolution of the behavior and vertical specialization, if effects from learning and external factors in the environment are indeed minimal.

The vertical distribution patterns and fidelity estimates derived from the trapping data (Chapter 2), as well as the climbing dispositions elucidated in the experimental study, appear to reflect well-defined patterns of vertical habitat specialization for each of the species. Within this behavioral specialization, morphological adaptations should evolve that contribute to survival and reproductive fitness (Endler,

1992; Futuyma and Moreno, 1988). In Chapter 4 I examine one potential adaptation, pelage color, and its potential function in crypsis from visually hunting predators.

CHAPTER 4 COLORATION

Introduction

Natural selection for animal coloration that matches the background of the habitat is common among organisms that are preyed on by visually hunting predators (Cott, 1940; Endler 1986b). Although nocturnal mice are active at times when vertebrate vision is limited by low light intensities, background matching has been demonstrated for several nocturnal species that inhabit deserts and beaches (Benson, 1933; Dice and Blossum, 1937; Kaufman, 1974).

The mice of Monteverde live among a diversity of predator species that use vision to detect and kill prey (Table 1-3). If light levels in the forest are adequate for the perception of contrast differences, the mice should be subject to selection for background matching, even if active at night. Ecological specialization for vertical habitats dominated by the greens of the canopy or browns of the forest floor suggests that pelage colors should vary among species and show character states consistent with vertical specialization (Chapters 2 and 3).

Considering coat color as a significant signal to predators preying on nocturnal mice may seem counter-intuitive. Light levels at night, particularly in the forest, are not sufficient for color vision. Nevertheless, color as a signal should not be dismissed without consideration. In Monteverde when the moon is full and the northeast trade winds sweep mist down from the Continental Divide, conditions are often right to see a "moonbow," a nocturnal rainbow. The human eye sees a silver arc of light, and although water droplets are separating the moonlight into the wavelengths of the visible spectrum, the colors are

indiscernible. The moonbow serves to illustrate two points: first, the physics of color still operate within the environment despite the low light levels, and second, although color signals reach the eye, night-time visual systems process the signals differently than day-time visual systems.

Night vision may appear in black and white, but the underlying mechanics are based on the sensitivity of the eye to wavelengths reflected from colored objects. Thus, to analyze the function of coloration in nocturnal mice, it is important to include the interaction of pelage reflectance spectra with the night-time perceptual abilities of the major predators (Endler, 1990; 1991; 1992). Analyses that consider nocturnal perception, however, are less complicated than those that concern color perception, because night vision among vertebrates is nearly identical. Rod cells most frequently are the basis of night vision in this group and the relative spectral sensitivity of rods is fairly uniform among species (Figure 4-1; Goldsmith, 1990). In contrast, color vision varies widely among diurnal vertebrate predators. Differences in the types of retinal cone cells, the spectral sensitivity of each type of cone cell, and the presence of colored oil droplets in the cornea, account for some of this variation (Goldsmith, 1990).

In addition to perceptual abilities, the color of light striking the object can affect the appearance of color spectra because objects differentially reflect and absorb particular wavelengths (Endler, 1990; 1991; 1992; Hailman, 1979; Hurvich, 1981). This is particularly important in nocturnal vision. Rod vision detects only the absolute brightness of spectra, not hue (violet, blue, green, yellow etc.) or chroma (the relative brightness of the dominant hue). Nevertheless, hue and chroma can affect perceived brightness because rods are most sensitive to middle wavelengths and least sensitive to long and short wavelengths (Figure 4-1). Thus a green object of the same absolute radiance as a blue or a red object would appear brighter than the other

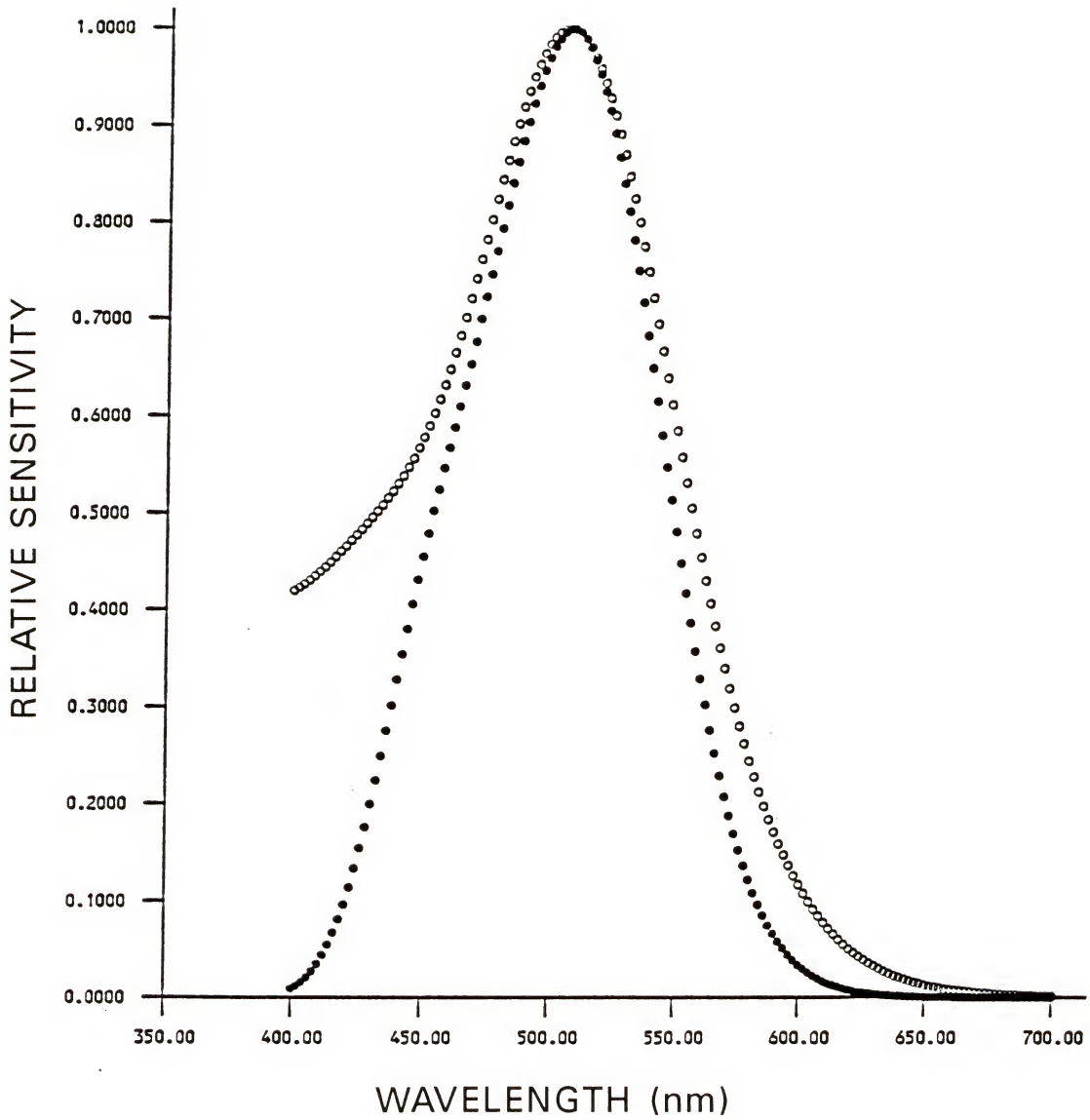


Figure 4-1. Spectral sensitivity curves for rod cells. Open dots = relative absorbance of photons by a typical rod cell (Endler, 1991). Closed dots = relative perceived brightness by humans under rod vision (Wyszecki and Stiles, 1982).

two objects at low ambient light intensities of rod vision. Slight changes in the brightness of reflectance spectra as a result of an interaction with even slightly colored ambient light may be significant to the detection of brightness differences because dark-adapted rod cells can respond to single photons of light (Barlow, 1957).

The common use of rod cells in vertebrate night vision, with its characteristic spectral sensitivity curve suggests that, despite the diversity of predators in Monteverde (Table 1-3), selection imposed on nocturnal prey by the perceptual abilities of visual nocturnal predators (Endler, 1992) should be fairly uniform among vertical as well as horizontal habitats. Differences in coloration among species, therefore, should evolve as a consequence of differences in factors in the environment in which individuals specialize (ambient light and background colors), rather than differences among species in the night vision of their major predators.

Research Overview

Endler (1991) incorporated both ambient light spectra and the spectral sensitivity curves of the retinal pigments of predators in an analysis of the appearance of guppy color patterns to diurnal predators. His results showed that differences in the spectral sensitivity of the predator's visual system, as well as the light environments guppies selected for display or foraging affected calculated measures of conspicuousness of the color patterns within the habitat. The results suggested that the observed color patterns were less conspicuous to predators at the times and places of foraging and more conspicuous to guppies at times and places of courtship. These same methods could provide insight into the question of the appearance of mouse pelage color to nocturnal predators and were used for these analyses.

I had three research objectives: 1) examine the populations of mice in the cloud forest community for color patterns associated with

vertical specialization, 2) explore how nocturnal light environments and the perceptual abilities of predators using night vision might affect the detection of mice against the backgrounds of the habitat using Endler's methods (1991), and 3) examine the observed color patterns and potential selective hypotheses within the context of what is known about the pigmentation process of mammals and the production of mammal color patterns.

The most appropriate light environments and backgrounds for each species included in the comparative analyses were chosen based on the results of the trapping study (Chapter 2) and escape experiments (Chapter 3). The research at Monteverde was conducted with John A. Endler of the University of California at Santa Barbara.

Materials and Methods

Color Measurement

Equipment. The irradiance spectra of ambient light and the reflectance spectra of mouse pelage and background substrates were measured using a spectroradiometer. The spectroradiometer recorded total light intensity, or photon flux (measured in $\mu\text{mol m}^{-2} \text{sec}^{-1} \text{nm}^{-1}$, $M=1$ mole or 1 Einstein = 6.022×10^{17} photons), at 2 nm intervals of the visible portion of the radiant spectrum (400–700 nm). Data were stored in the memory of a portable computer. In July 1989, a spectroradiometer sensitive to low light levels was used that could measure twilight and moonlight. The system was designed and constructed by John A. Endler (see Endler, in press). In July 1990, a LI-COR (Lincoln, Nebraska) model LI-1800 portable spectroradiometer was used that was more suitable for field use, but less sensitive to low light intensities. Both systems give identical results when run simultaneously in the field. Each was calibrated in the United States before and after the field work in Costa Rica using a LI-COR model LI-1800-02 optical radiation calibrator.

The color of ambient light. Ambient light of the forest understory was measured with the spectroradiometer fitted with a LI-COR LI-1800 cosine receptor head. The cosine receptor receives and senses light from all angles of a 180° hemisphere and measures irradiance, the photon flux per unit area arriving from numerous directions.

Measurements were taken on the understory trapping transect in Campbell's Woods with the spectroradiometer mounted on a tripod approximately 1 m above the forest floor. Repeated scans were made in each of the light environments described by Endler (in press; 1992) as characteristic of forest habitats. These light environments are independent of geography or species composition of the forest and are defined by the geometry of light paths through the canopy, weather conditions, and time of day. The seven light environments measured were forest shade (continuous canopy above), woodland shade (discontinuous canopy above), small gaps ("sunflecks" <1 m in diameter), large gaps (areas of direct sunlight with little or no interception by the canopy), sunset/sunrise, twilight, and moonlight. Daytime scans were made under conditions of full sun and clouds at various times of the day. Light levels in the forest after twilight were beyond the sensitivity of the spectroradiometer and spectral curves of moonlight derived from scans in open areas were used to approximate this light environment. Ambient light along the vertical profile of the forest was not measured due to logistic constraints. Since the spectral composition of ambient light was shown by Endler (in press) to be predicted by the geometry of the light path through the forest, weather, and sun angle, the same geometries evident across the forest landscape also apply to the vertical profile (Endler, in press). Endler confirmed the existence of the same light environments along a vertical transect at a tower (Endler, in press) on Barro Colorado Island, Panama, as well as within shrubs (Endler, pers. comm). Forest shade and small gaps were found in the lower strata where the canopy remained continuous and woodland shade

and large gaps predominated in the upper strata when the canopy became discontinuous. Sunset/sunrise and twilight spectra were the same in forest as well as in open areas and will appear the same throughout the vertical strata (Endler, in press).

Color reflectance of mouse pelage. Animals captured in the morning on the understory transect were taken back to a field laboratory, measured for color reflectance as they were hand-held under the spectroradiometer, and then released later that same day at their site of capture. Pelage was illuminated with an automobile headlamp powered by a motorcycle battery. Care was taken to shield the eyes of each individual. Reflectance scans were taken on four areas of the body: flank, rump, back, and venter. The back area approximated the view presented to a predator above the animal, while the rump approximated the view presented to a predator following the animal. The flank was defined as the area of brightest pigmentation dorsal to the lateral line separating the dorsum and venter. Since it was difficult to hold the animals for the length of time required to make a scan, replicates within individuals were made only if the animal moved or it appeared from a sighting behind the lens that the first scan may not have captured maximum reflectance.

Color reflectance of the pelage was measured as radiance (photon flux per unit area reflected from one direction) with a radiance attachment to the spectroradiometer that consisted of a lens at the end of a fiber optic probe that allows focussing on a narrow and well-defined area on the animal or background. Pelage scans were made with the lens accepting light from a 10° angle, focussed on an area approximately 1 cm in diameter. A white standard was scanned before pelage measurements.

Most measurements were taken in the visible spectrum from 400 to 700 nm. On several individuals we measured from 400 to 900 nm to examine reflectance of wavelengths beyond the visual spectrum into near-

infrared wavelengths. Measurements into the ultraviolet required additional procedures with ultraviolet illumination and were not taken during the sessions.

Color reflectance of background substrates. The same methods were applied to the measurement of the color reflectance of background substrates. Specimens of live and dead plant material and soil were collected along the understory transect and from the crown and trunk of several canopy trees. The specimens were grouped into the following broad categories: soil, live leaves, senescent leaves, unhealthy leaves, light dead leaves, dark dead leaves, reddish leaves, green twigs, light gray twigs, dark twigs or branches, lichen and/or fungus encrusted on bark, rotting bark, green moss, reddish moss, and epiphyte mats.

The color of individual specimens was measured under three conditions common to the cloud forest: 1) dry, with no standing water on the surface, 2) wet, with a thin film of water on the surface and positioned such that color, not glare, was reflected to the spectroradiometer, and 3) wet, positioned with a thin film of water reflecting glare from the specimen's surface. The specimens were positioned by sighting directly through the lens.

Comparative Analyses

Standardizing spectra for comparative analysis. For comparative analyses, the radiance measures of mice and backgrounds were adjusted for effects from variance in the color and intensity of the illuminating and ambient light of the laboratory (Endler, 1990). The radiance of a white reflectance standard, barium sulphate, was measured under the same lighting conditions as the mice and backgrounds. Scans of the standard were made several times during a session to adjust for possible changing light conditions. For each radiance measure, the total brightness at each wavelength interval was divided by the total brightness of the corresponding wavelength of the white standard. This ratio of

reflectance was then multiplied by the known reflectance spectrum of the white standard. The resulting absolute reflectance spectrum describes the ratio or fraction of incident light at each wavelength interval that will be reflected back to the viewer due to the reflective properties of the object when viewed under pure white light.

To compare hue or chroma, the shape of the reflectance spectrum independent of its total brightness is of interest. To standardize spectra for these analyses, the absolute reflectance spectra were divided at each wavelength interval by the total light intensity of the entire spectrum, producing a spectrum with the same shape but with a total intensity equal to $1.0 \mu\text{mol m}^{-2} \text{sec}^{-1}$ (Endler, 1991; 1992). A spectrum characteristic of each species, background type, and light environment was then estimated by averaging the standardized spectra at each wavelength interval. Standard deviations around the mean of each wavelength interval were calculated to estimate variation.

Quantitative measures of spectra characters. The term color, as used hereafter, is defined as the shape of the visible spectrum, and it can be used to compute hue, chroma, and brightness. Quantitative values were calculated following the methods outlined by Endler (1990).

Brightness, the number of photons that produces the spectrum, is equal to the area under the curve and was calculated by integrating the curve. Hue and chroma, independent of brightness, were computed for each standardized spectrum using a segment color classification (Endler, 1990). The method is based on differences in the relative abundance of photons among four equally spaced segments of the visible spectrum (Blue=400-475 nm, Green 475-550 nm, Yellow 550-625 nm, Red=625-700 nm), and approximates the chromatic response functions of the opponent-process of color vision (Hurvich, 1981). Endler (1990) has demonstrated that principal component analysis of natural color spectra, using the intensity at each wavelength interval as a variable, identify three or four eigenvectors with shapes that are also similar to the shape of the

chromatic response functions. Segment classification is equivalent to making step functions out of the eigenvectors, but is simpler to calculate and the axes are independent of the data set, making comparisons among objects in their position in color space possible (Endler, 1990).

After the spectra were divided into segments, the total brightness of each segment was calculated, and then standardized by dividing by the brightness of the entire spectrum. Comparisons in brightness were made between long-medium wavelengths (LM) and medium-short wavelengths (MS):

$$LM = \text{Red} - \text{Green}$$

and

$$MS = \text{Yellow} - \text{Blue}$$

LM was then plotted as a function of MS, and graphically shows where the spectrum falls in "color space" relative to other color spectra (Endler, 1990). Hue is estimated by the angle clockwise from the positive Y-axis (LM) of color space. Pure colors will fall on one of the four axes--red (0°), yellow (90°), green (180°), and violet (270°), while intermediate colors fall between the axes. Chroma is estimated by the euclidean distance of the plotted point from the origin. Colors with greater chroma appear farther from the origin, while colors with less chroma cluster at the origin. Colors mixed with black or white have less chroma, and will cluster around the origin, regardless of their brightness.

Comparing color and brightness of pelage and background.

Comparisons of the color of pelage and backgrounds were made by deriving the segment coordinates from standardized reflectance spectra, plotting the coordinates in color space, and examining for overlap. Perceived brightness matching during night vision was analyzed by first correcting for the interaction of reflectance spectra and ambient light spectra. The mean reflectance at each wavelength interval (fraction of photons

reflected at that interval) for each species and each background type was multiplied by the mean irradiance at each wavelength interval of the characteristic ambient spectra measured within the habitat. Ambient light spectra were adjusted to the same total intensity at $10 \mu\text{mol m}^{-2} \text{sec}^{-1}$. Perceived brightness differences were calculated by finding the integral of the resulting spectra and calculating the difference between pelage and background.

The interaction of the resulting spectra reaching the surface of the eye with the rod cells of the retina was then examined by including a correction factor for the spectral sensitivity of the rod cells. The mean reflectance spectra of each species and each background type corrected for effects from different light environments was multiplied at each wavelength interval by the corresponding sensitivity function of a rod cell (Figure 4-1; Endler, 1991). This function is a photon capture rate for a single rod cell, ignoring subsequent processing by the visual system. The resulting reflectance spectra and differences between species and background types calculated. Similar analyses could be conducted for diurnal comparisons, incorporating the sensitivity curves of the photopic pigments of diurnal predators (Endler, 1991). Since the actual predators responsible for diurnal predation are unknown, and the number and sensitivity curves of the cone cells vary among species, such an analysis was beyond the scope of this study.

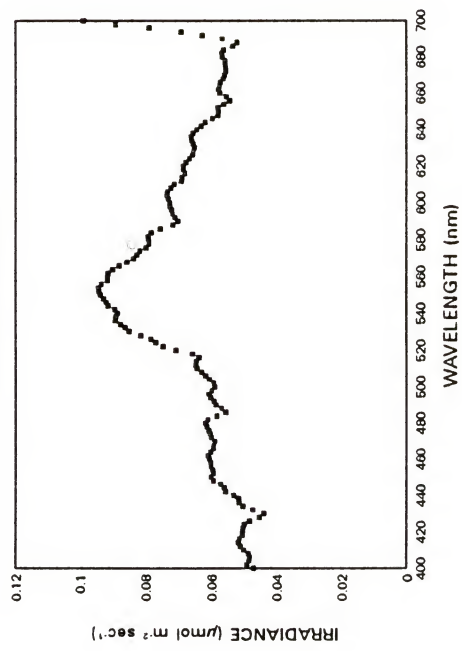
Results

The Colors of Ambient Light

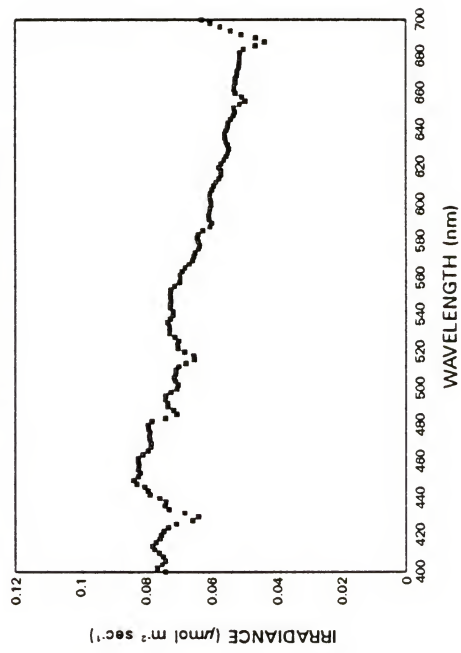
Ambient light spectra in Campbell's Woods were consistent with the major light environments described by Endler (1992; in press) (Figure 4-2, A-G). Continuous canopy dominated the study site, and the average ambient light spectrum in the forest shade of the understory when illuminated by the sun was yellow-green in hue (Figure 4-2A), primarily due to the reflectance of green wavelengths from chlorophyll. In areas

Figure 4-2. Mean irradiance spectra for the seven light environments standardized for the same total brightness. A. Forest shade, B. Woodland shade, C. Small gaps, D. Open/cloudy, E. Purple twilight, F. Red sunrise/sunset, G. Moonlight.

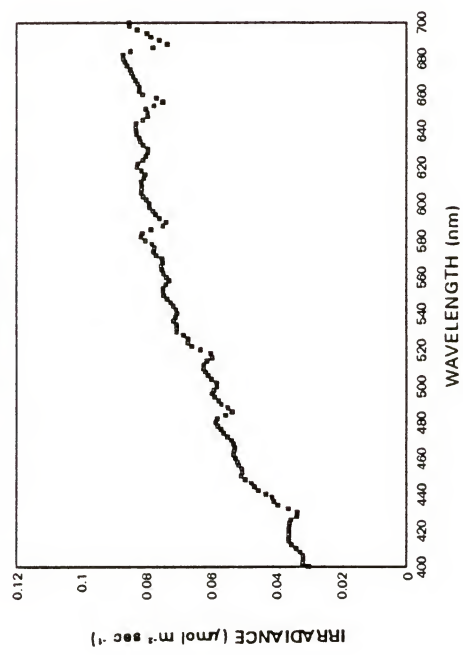
A. FOREST SHADE



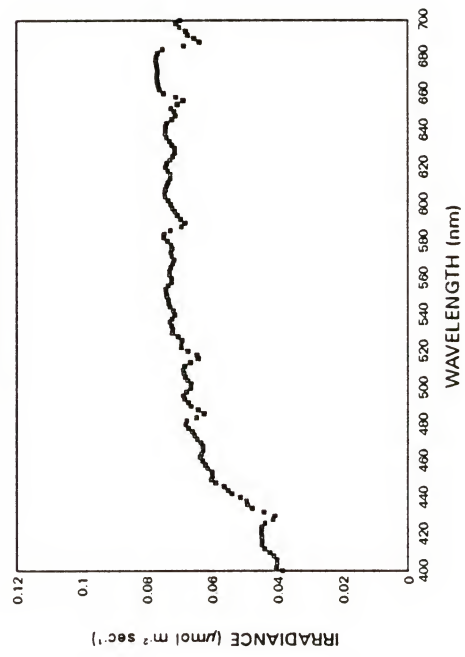
B. WOODLAND SHADE



C. SMALL GAPS



D. OPEN/CLOUDY



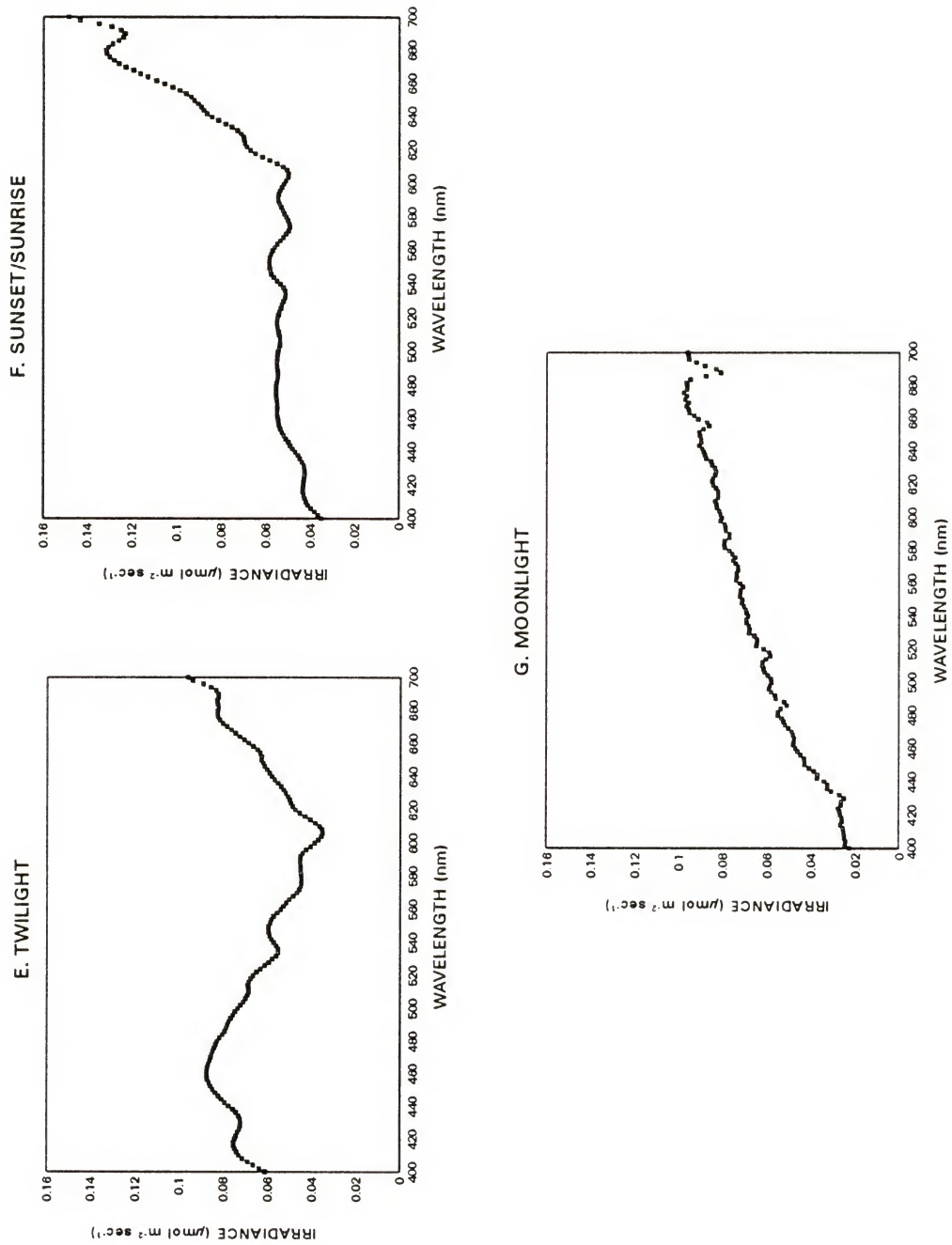


Figure 4-2--continued

of discontinuous canopy (woodland shade) light was blue-gray in color (Figure 4-2B), primarily due to greater irradiance from blue sky and less reflectance from green leaves. Small gaps ("sunflecks") were reddish (Figure 4-2C) while large gaps were similar to spectra in open areas, which were white (Figure 4-2D).

Under cloudy conditions, however, understory light (including continuous canopy, discontinuous canopy, and small gaps) was white with a relatively flat spectral curve, similar to light in open areas under full sun (Figure 4-2D). Mist scatters light, producing diffuse white light that predominates and masks the color effect from the reflectance of green leaves or blue sky.

The spectrum of ambient light changed considerably and rapidly at twilight with marked differences in brightness, hue, and chroma. Dawn and dusk in the forest, as well as in the open, under cloudy or clear conditions, demonstrated the same sequence of color changes. There was a rapid change in brightness at twilight, and with the low sun angle and the longer light path travelled through the atmosphere, ozone absorption of wavelengths in the orange portion of the spectrum became apparent (McFarland and Munz, 1975). Red and blue wavelengths predominated, producing light with a purple cast (Figure 4-2E). In the presence of clouds and/or dust the longer red wavelengths were reflected to the ground producing a short period of red light (Figure 4-2F). Moonlight, measured by necessity outside of the forest, was richer in the longer wavelengths (yellowish-red) (Figure 4-2G).

The Colors of Mice

To the human eye, the dorsa of the mice ranged from gray to brown to reddish-brown, whereas the venters were gray or white. The measured absolute reflectance spectra, including venters, were relatively flat in the blue and green portion of the spectrum, with gradual increases in reflectance toward the longer red wavelengths (Figure 4-3). The

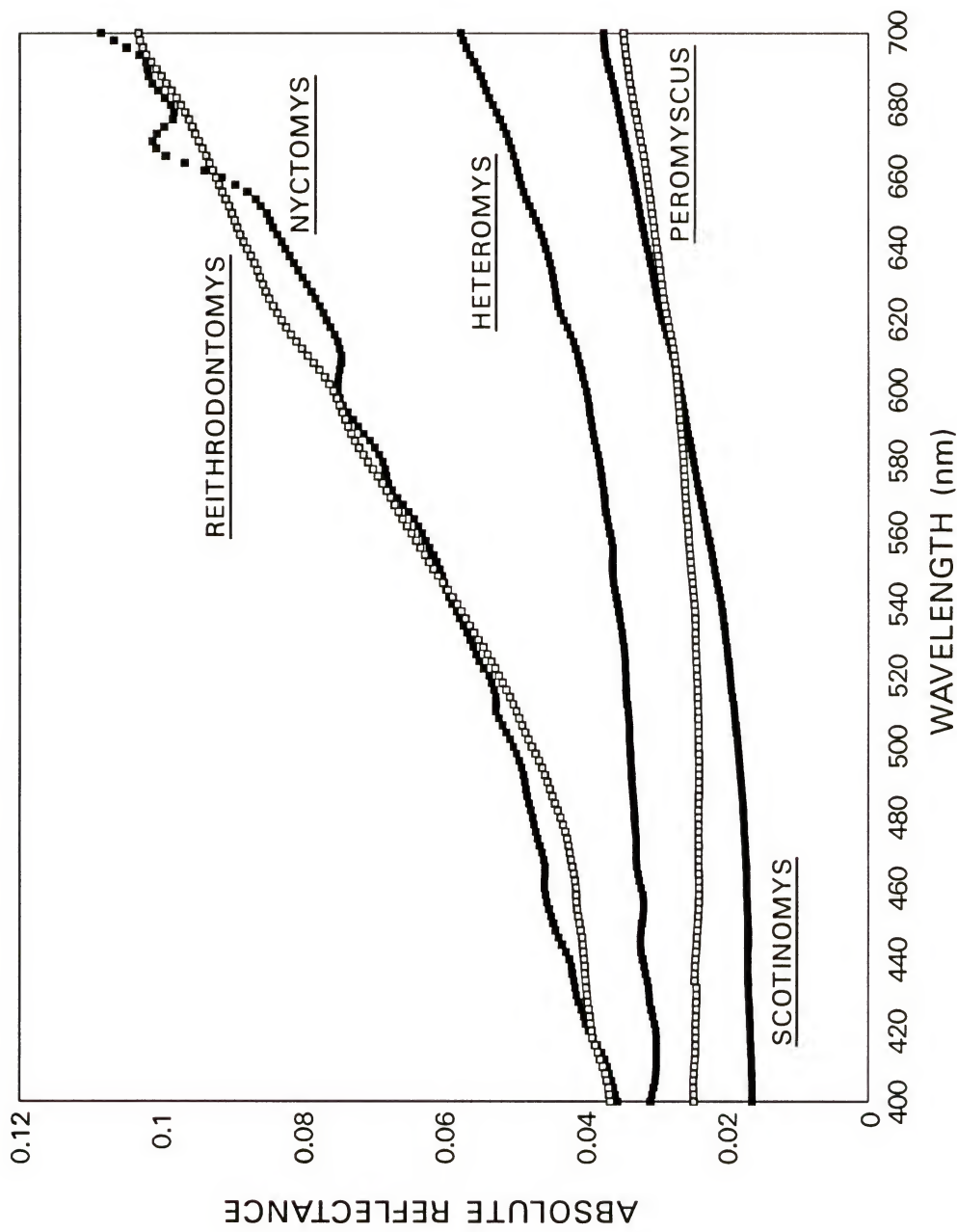


Figure 4-3. Mean reflectance spectra of the backs of the five species of mice. Absolute reflectance represents the fraction of incident light at each wavelength reflected back to the viewer if pelage were illuminated by perfectly white light (total intensity = $1.0 \mu\text{mol m}^{-2} \text{sec}^{-1}$).

brightest reflectance spectra were mid-ventral, followed by the flank, rump, and back. Nyctomys sumichrasti and R. gracilis, the two arboreal species, showed brighter dorsal reflectance spectra, while the terrestrial species were darker (Figure 4-3 and 4-4).

There was variation in spectra among individuals, but this variation represented small-scale differences in reflectance at each wavelength rather than large scale differences in the shape of the spectral curve. Variance was least at the shorter wavelengths, increasing with longer wavelengths.

Several patterns emerged when spectral coordinates were calculated from standardized reflectance spectra and plotted in color space (Figure 4-5 and 4-6). First, all species are orange-yellow in hue and fall within a narrow band of the orange/yellow quadrant of color space. A similar angle of deflection from the red-axis is seen in the points derived from the mean reflectance spectrum of each species (Figure 4-5) as well as in the points derived from the reflectance spectra of individual scans regardless of species or location on the body (Figure 4-6). Peromyscus nudipes and H. desmarestianus clustered near the origin of color space (low chroma) and are gray, but again with a similar reddish hue. Ventral spectra, which were white or gray to the human eye, were also included in Figure 4-6 and clustered along the same angle of deflection from the X-axis showing a similar hue as dorsal spectra. Overall, there was little variation in hue among individuals and species.

Second, chroma, as measured by the euclidean distance of the spectrum from the origin (Endler, 1990), varied, but in species-typical patterns (Figure 4-5). The arboreal R. gracilis and N. sumichrasti showed greater chroma, while the terrestrial species, P. nudipes and H. desmarestianus show the least. The diurnal and terrestrial Scotinomys teguina, despite being the darkest of the species, was intermediate to

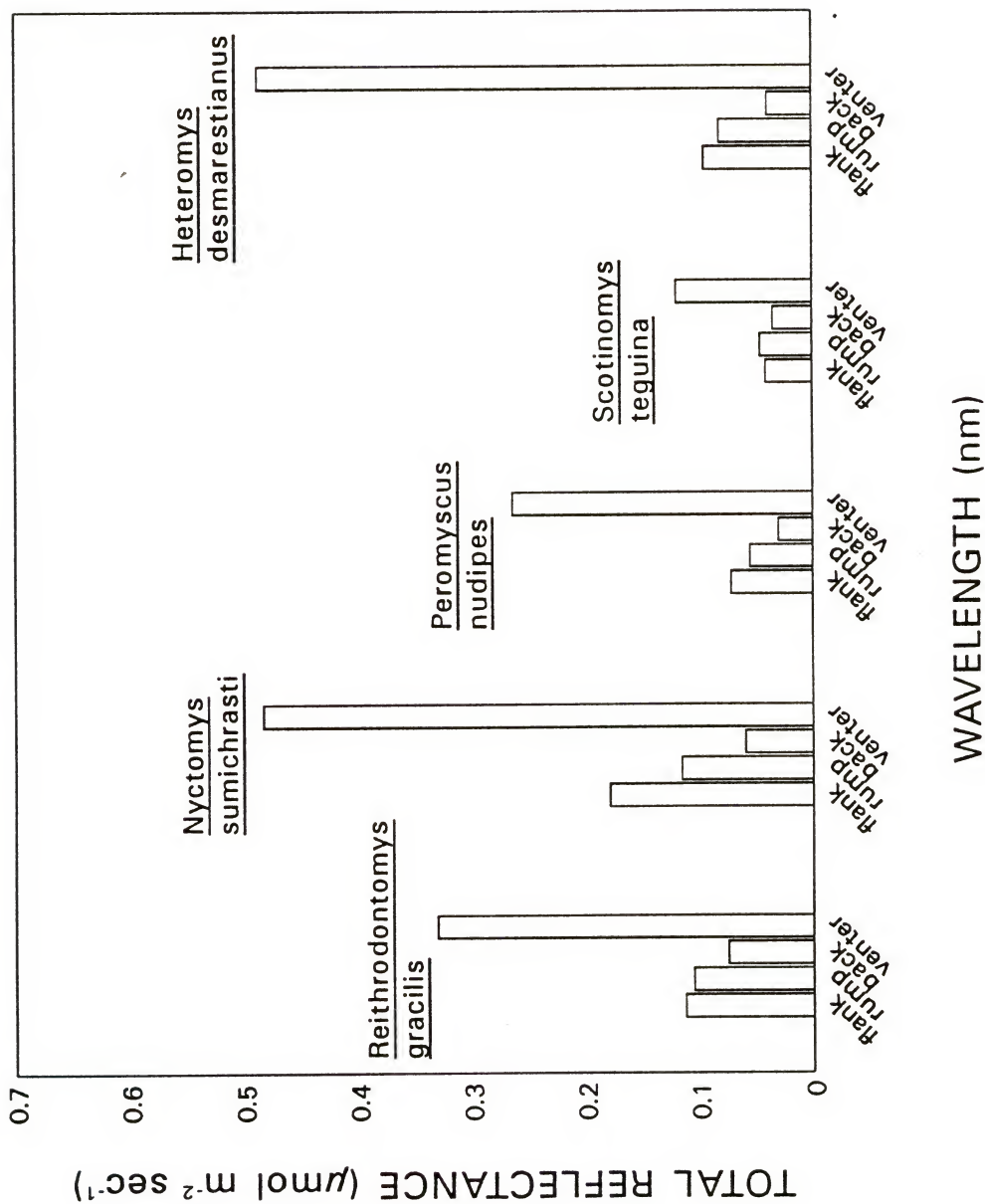


Figure 4-4. Mean brightness of the flank, rump, back, and venter of each species. Total reflectance is the total number of photons reflected from the fur if pelage were illuminated by perfectly white light (total intensity = 1.0 $\mu\text{mol m}^{-2} \text{sec}^{-1}$).

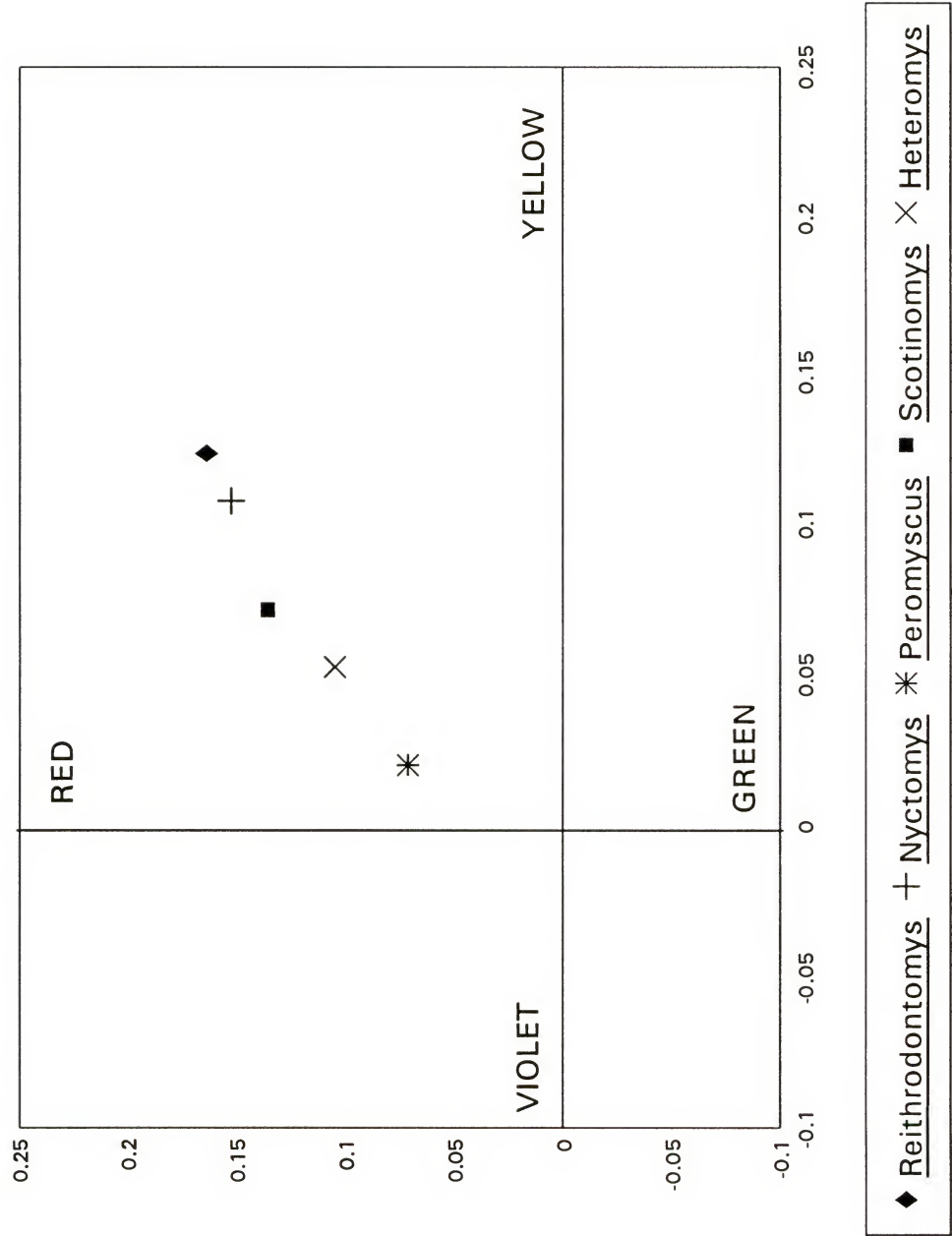


Figure 4-5. Segment classification of the mean reflectance spectrum of the backs of mice. Each point shows a similar angle of deflection from the red axis of color space (see text), indicating that the species are of a similar orange/yellow hue. The Euclidean distance from the origin, however, differs among species. Points closer to the origin indicate the spectra have low chroma. Points farther from the origin indicate spectra with high chroma.

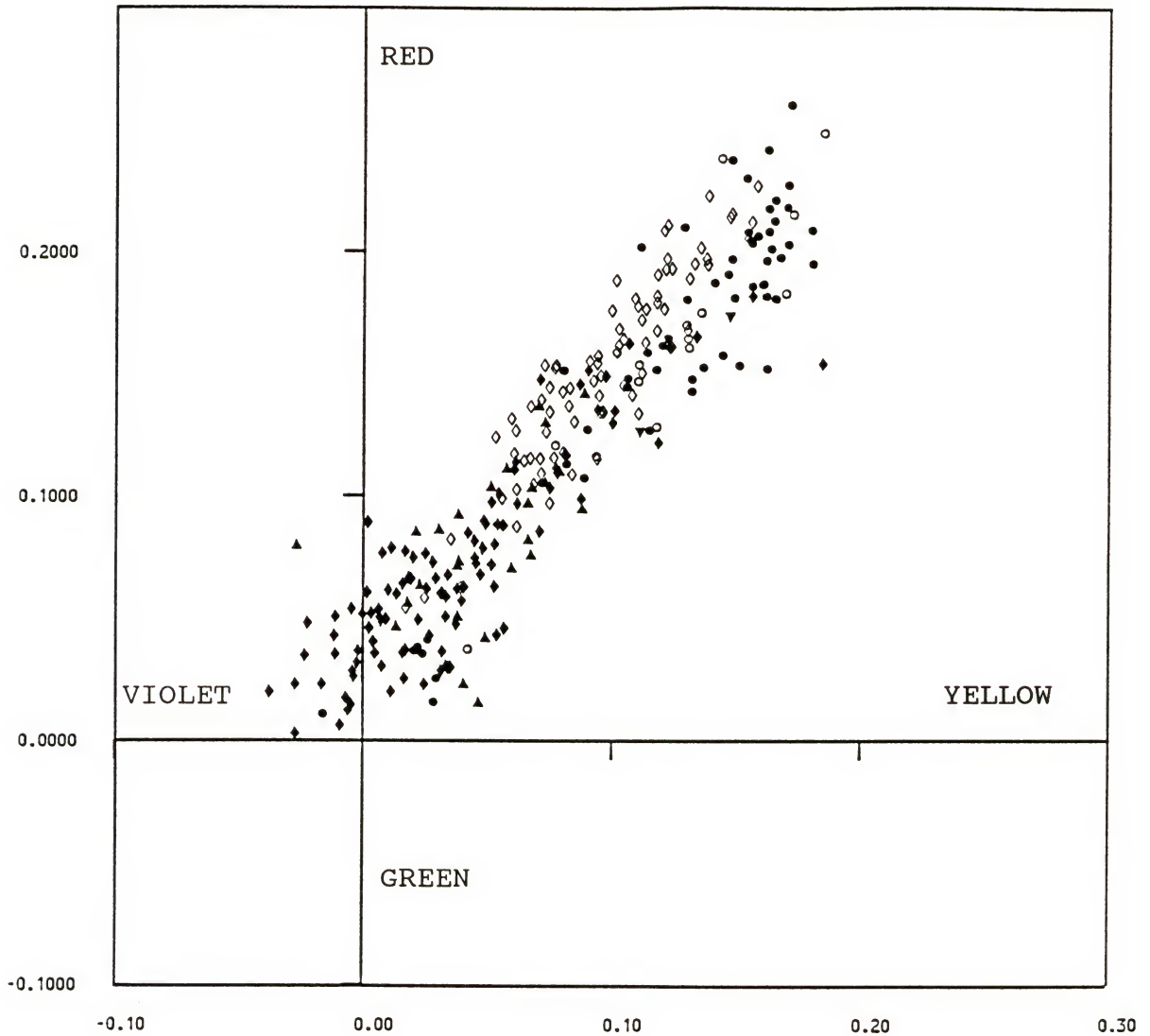


Figure 4-6. Segment classification of individual reflectance spectra (flank, back, rump, and venter) plotted in color space. Closed dots = *Reithrodontomys gracilis*. Open dots = *Nyctomys sumichrasti*. Closed diamonds = *Peromyscus nudipes*. Open diamonds = *Scotinomys teguina*. Triangles = *Heteromys desmarestianus*.

the arboreal and terrestrial species, showing greater chroma than its nocturnal counterparts on the ground.

The Colors of Backgrounds

Color spectra of backgrounds showed a broader range in hue and chroma. Wet and dry specimens plotted in color space fill a large portion of the orange/yellow and yellow/green quadrant (Figure 4-7). Wet conditions had a marked effect on background spectra. Note that the average distance from the origin is greater in the wet samples (Figure 4-7). A thin film of water on the surface decreased total brightness but increased chroma; greens became greener and reds became redder. Small irregularities on the specimen surface that scatter light, such as pits or scratches, are eliminated by a film of water, increasing chroma. If glare was reflected back to the spectroradiometer, reflectance was brighter, but the color was washed out as chroma decreased. Most of the points clustering near the origin are spectra with glare.

Comparisons of Mice Against Backgrounds

Color matching. When the segment coordinates derived from the reflectance spectra of the mice and wet/dry backgrounds are plotted together in color space, there is some overlap, but no clearly defined pattern of pelage matching background in reflectance spectra (Figure 4-8). Mouse pelage with greater chroma (particularly S. tequina, R. gracilis, and N. sumichrasti) fall within the range of hue and chroma found among orange/yellow backgrounds of the study site.

These spectra were measured within the visible spectrum (400-700 nm), but it is possible that animals may reflect infrared, similar to the infrared reflection of green leaves (Cott, 1940; Dodd, 1981; Schwalm et al., 1977). None of the species of mice, however, reflected strongly in the region of the spectrum above 700 nm.

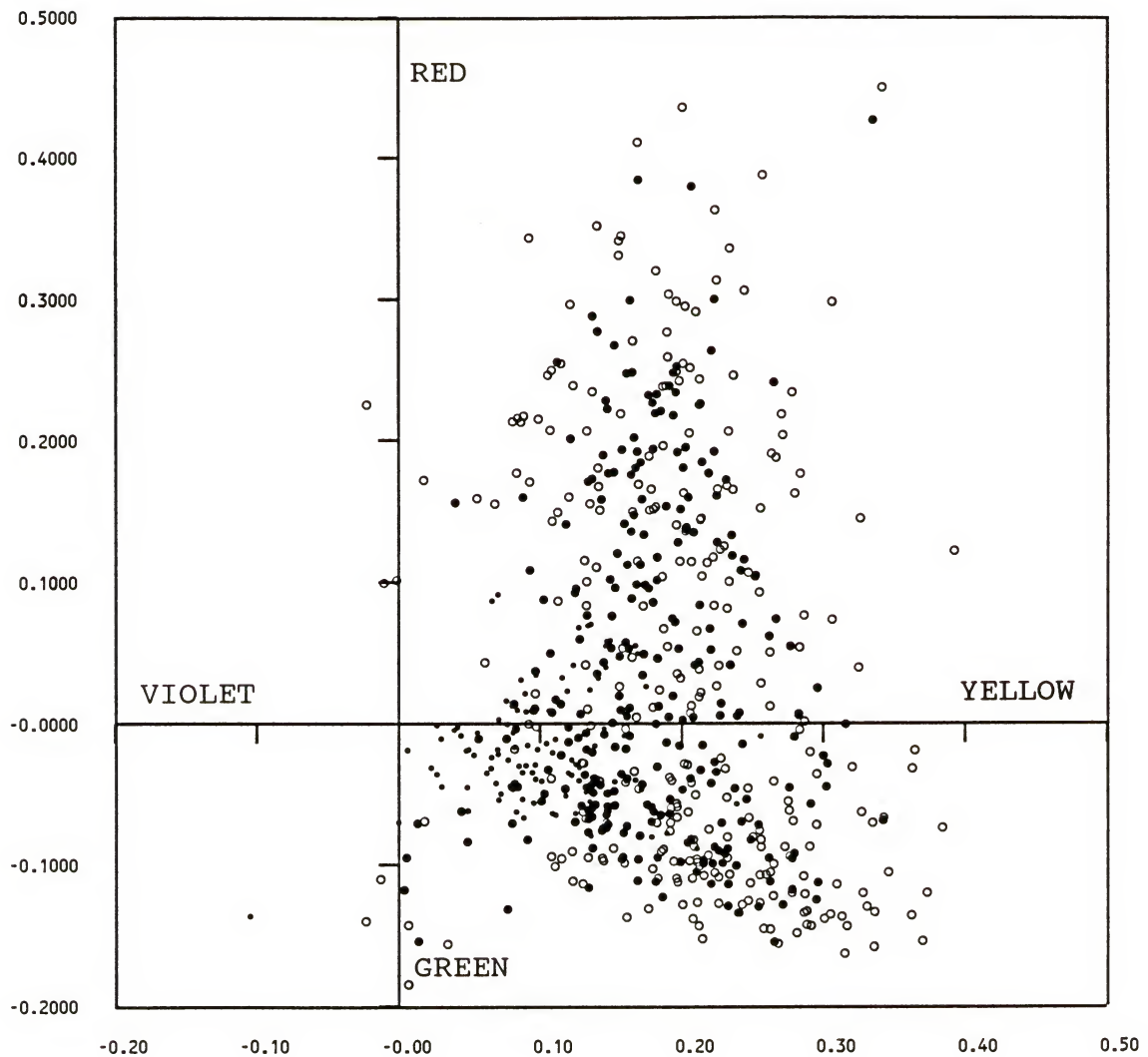


Figure 4-7. Segment classification of background reflectance spectra plotted in color space. Closed large dots = dry backgrounds. Open dots = wet backgrounds. Closed small dots = backgrounds with glare.

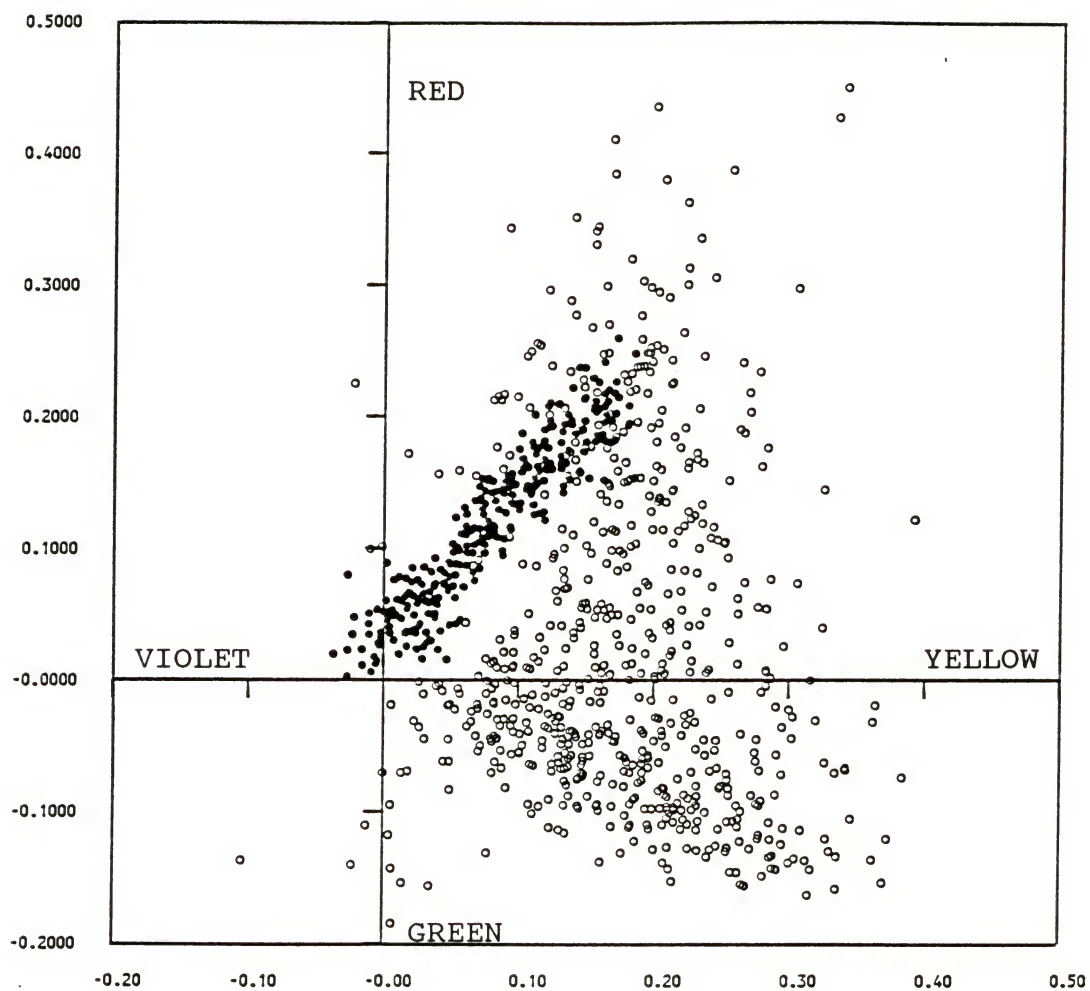


Figure 4-8. Segment classification of pelage and background spectra plotted in color space. Closed dots = pelage. Open dots = background.

Changes in brightness with light environment. Radiance spectra of each species were examined for differences in brightness when viewed within the six light environments that may be encountered by mice prior to the Purkinje shift to rod vision: forest shade, woodland shade, open/cloudy, small gaps, sunrise/sunset, and twilight (Figure 4-9). Mean brightness of pelage for all species under light environments adjusted to $10 \mu\text{mol m}^{-2} \text{sec}^{-1}$ was greater in light environments rich in long wavelengths (reddish light, small gaps, sunrise/sunset, and moonlight) and less in environments rich in short wavelengths (bluish light, woodland shade, and twilight). Reddish backgrounds such as soil showed similar patterns (Figure 4-10). Green leaves, however, were brightest in forest shade, less bright in reddish light environments (sunrise/sunset and moonlight), and darkest in light environments that were bluish (woodland shade and purple twilight) (Figure 4-10). The differences in brightness appear slight, but small differences may produce perceptual effects by the visual system that can vary by an order of magnitude. This is particularly true in the case of night-vision, where dark-adapted rod cells can respond to single photons of light (Barlow, 1957).

Differences between mean brightness of radiance spectra of pelage and backgrounds were calculated based first on the effects of ambient light at sunrise/sunset, twilight, and moonlight and then again including effects from the spectral sensitivity of the rod cells (Figure 4-11). The apparent brightness match of dorsal pelage improved for all species against all backgrounds in the three nocturnal light environments when the spectra were corrected for scotopic vision.

Reithrodontomys gracilis was brighter than most backgrounds, but the brightness difference between green twigs and/or light twigs decreased to a small amount under rod vision. However, it was not a particularly good match to soil, dead leaves, or rotting bark. Nyctomys sumichrasti showed a better brightness match to several backgrounds,

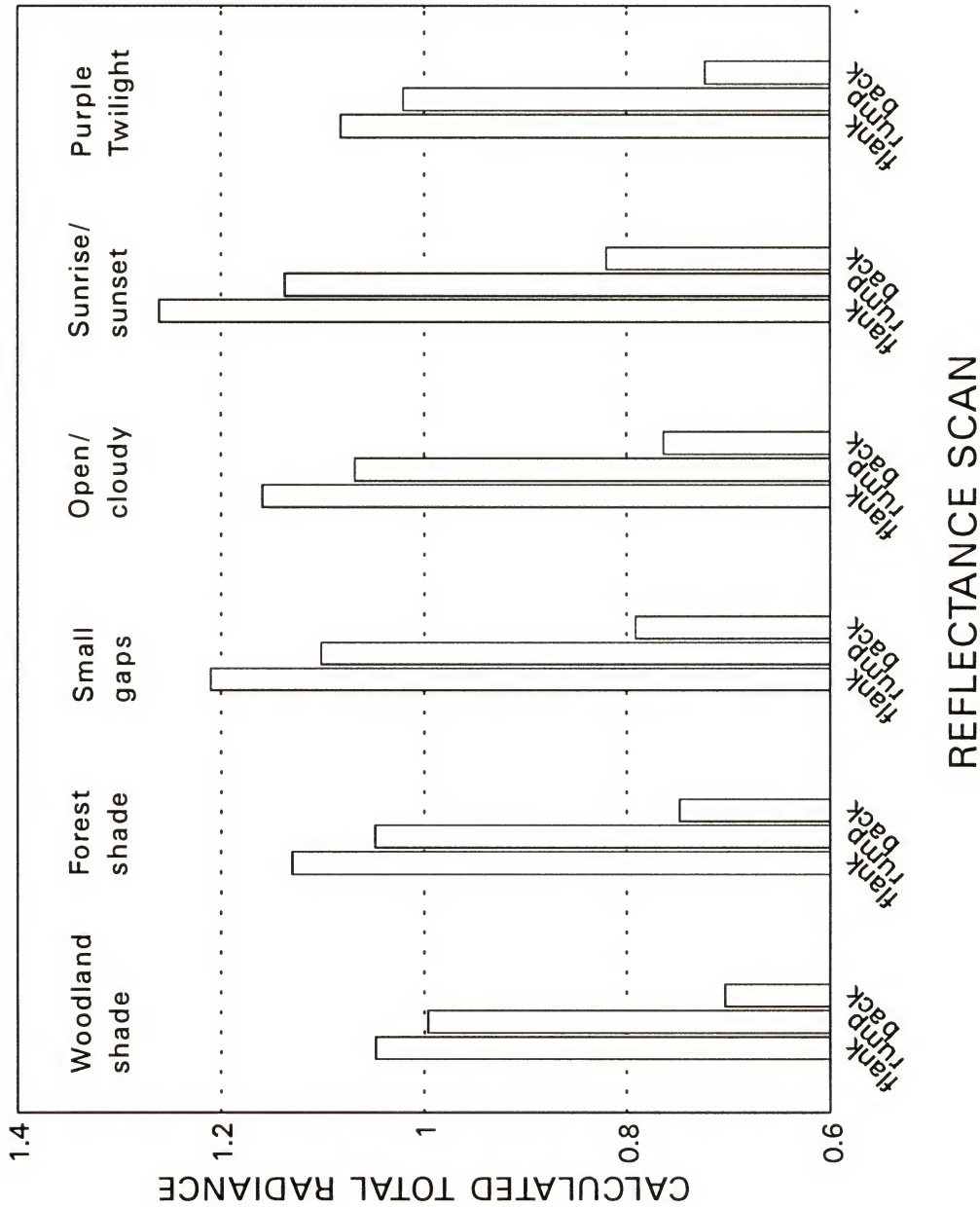


Figure 4-9. Brightness of the mean pelage spectra of *Reithrodontomys gracilis* when viewed in th different light environments. Total intensity of the six light environments adjusted to 10 $\mu\text{mol m}^{-2} \text{sec}^{-1}$.

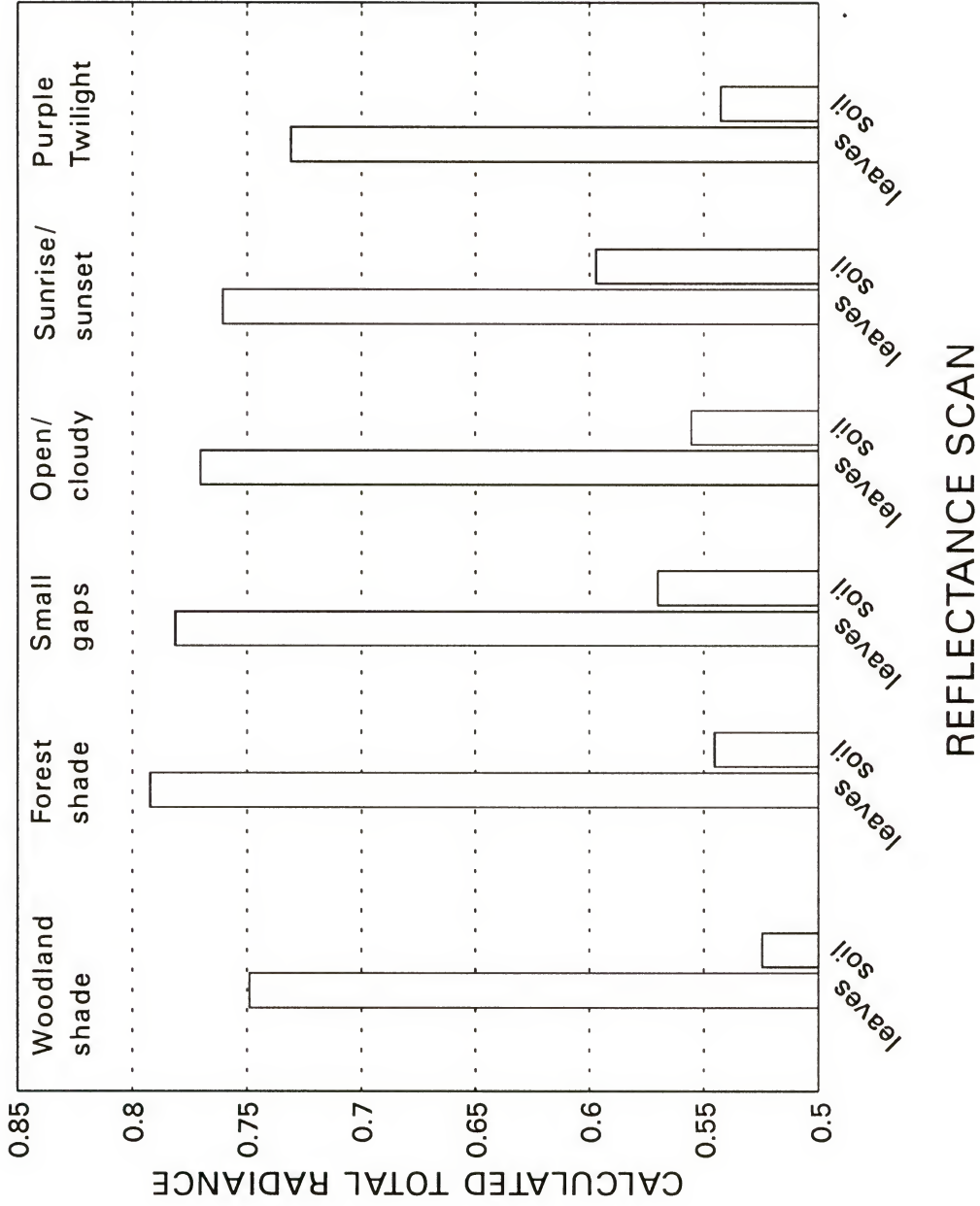
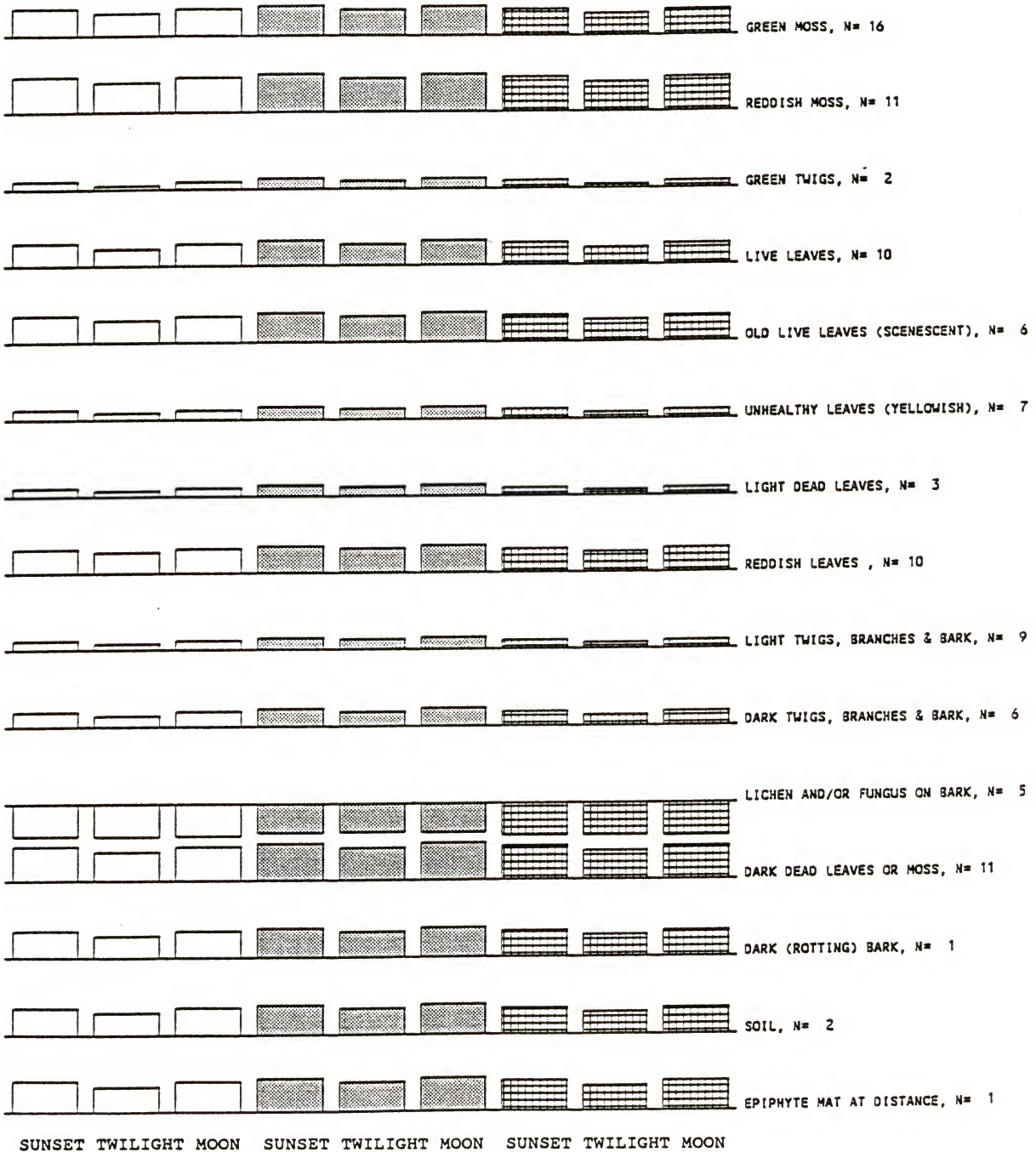
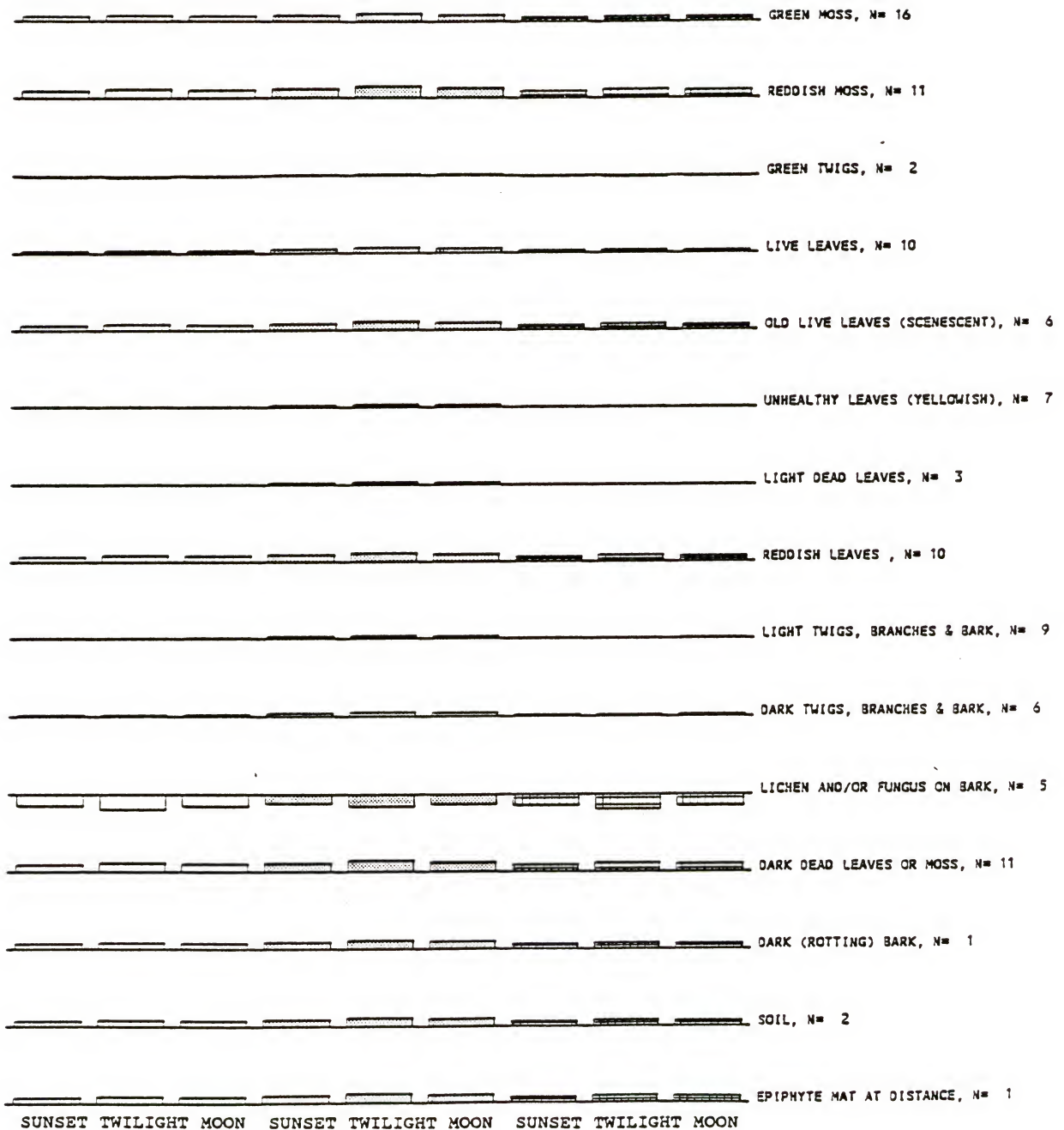


Figure 4-10. Brightness of green leaves and soil when viewed in the different light environments. Total intensity of the six light environments was standardized to $10 \mu\text{mol m}^{-2} \text{sec}^{-1}$.

Figure 4-11. Calculated brightness differences between pelage and background types under three nocturnal light environments for: A-B. Reithrodontomys gracilis. C-D. Nyctomys sumichrasti. E-F. Scotinomys teguina. G-H. Peromyscus nudipes. I-J. Heteromys desmarestianus. The first diagram for each species is the calculated brightness difference before incorporating effects from the rod spectral sensitivity curve; the second diagram for each species is the difference after calculations for rod vision. Rows are background classes. Columns are type of pelage, arranged in three groups: flank, rump, and back. Within each pelage group, the bars represent the value of the difference in calculated brightness within the sunset, twilight, and moonlight environments. The horizontal line in each row is $0.0 \mu\text{mol m}^{-2} \text{sec}^{-1}$, indicating a perfect match in brightness. Bars above the X-axis represent pelage brighter than background; bars below the X-axis represent pelage darker than background. The vertical scale on all graphs is identical for comparative purposes.

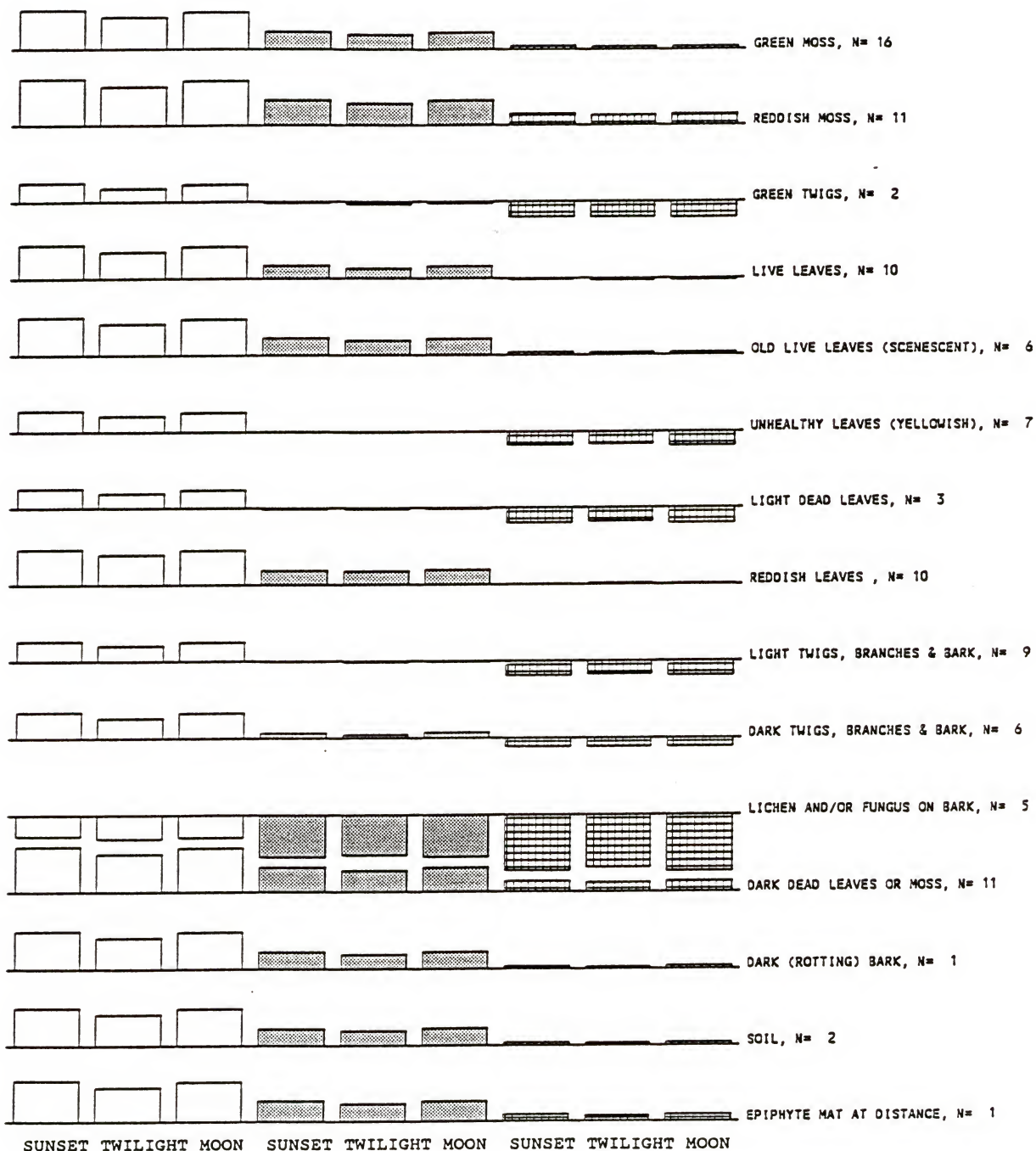
A. Reithrodontomys gracilis

CALCULATED BRIGHTNESS DIFFERENCES
WITHOUT EFFECTS FROM ROD VISION

B. Reithrodontomys gracilis

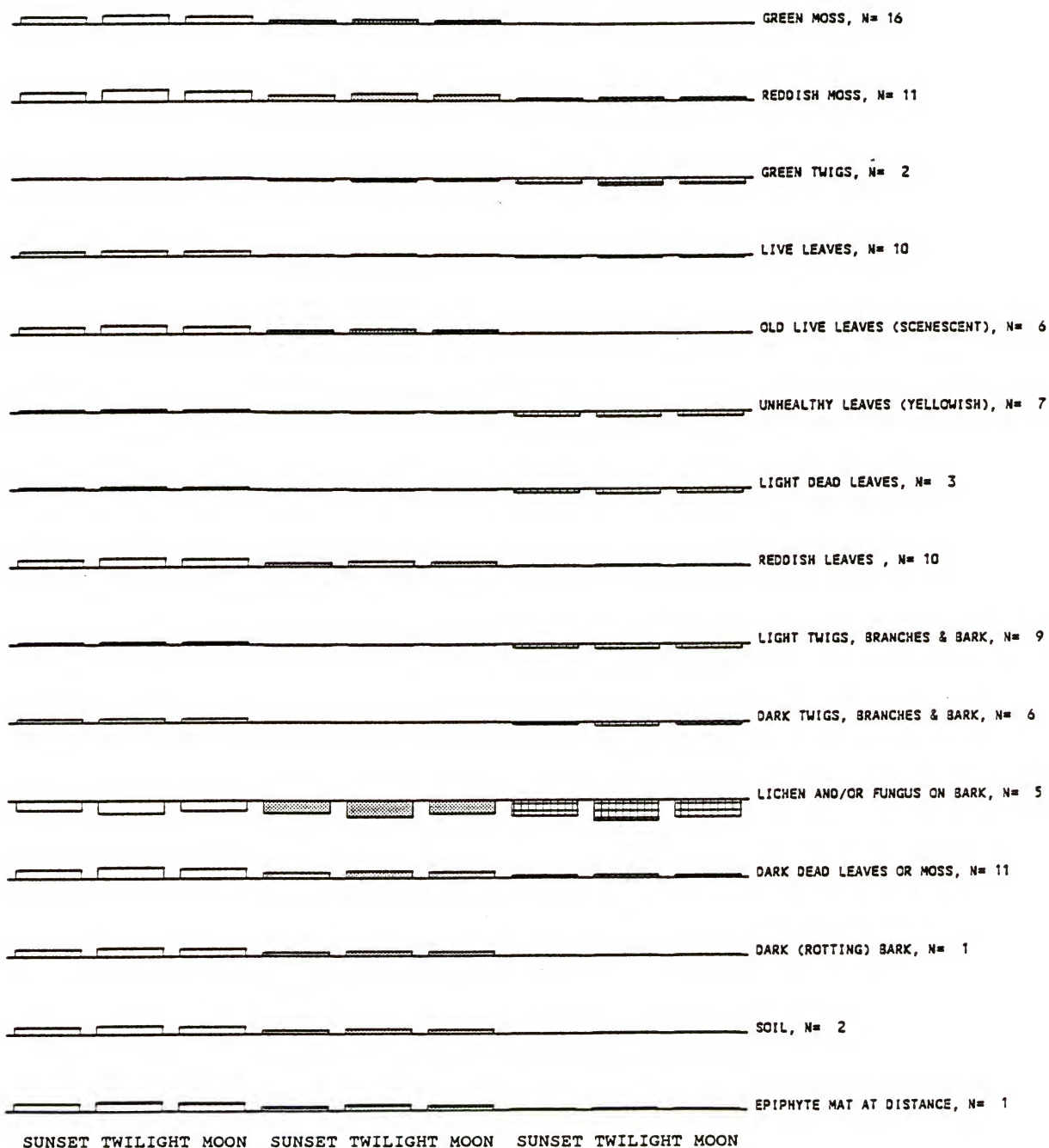
CALCULATED BRIGHTNESS DIFFERENCES
UNDER ROD VISION

Figure 4-11--continued

C. Nyctomys sumichrasti

CALCULATED BRIGHTNESS DIFFERENCES
WITHOUT EFFECTS FROM ROD VISION

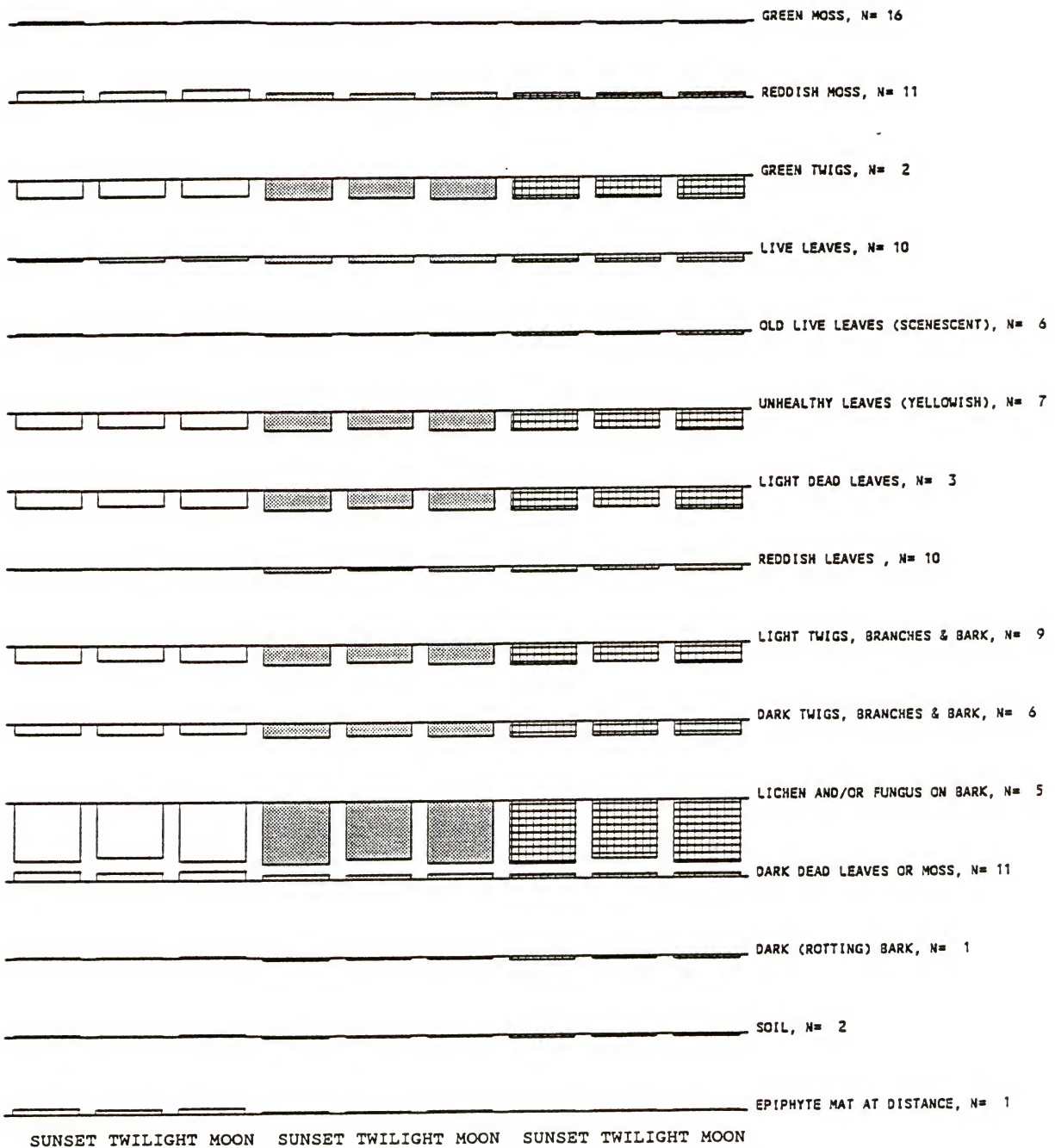
Figure 4-11--continued

D. Nyctomys sumichrasti

CALCULATED BRIGHTNESS DIFFERENCES
UNDER ROD VISION

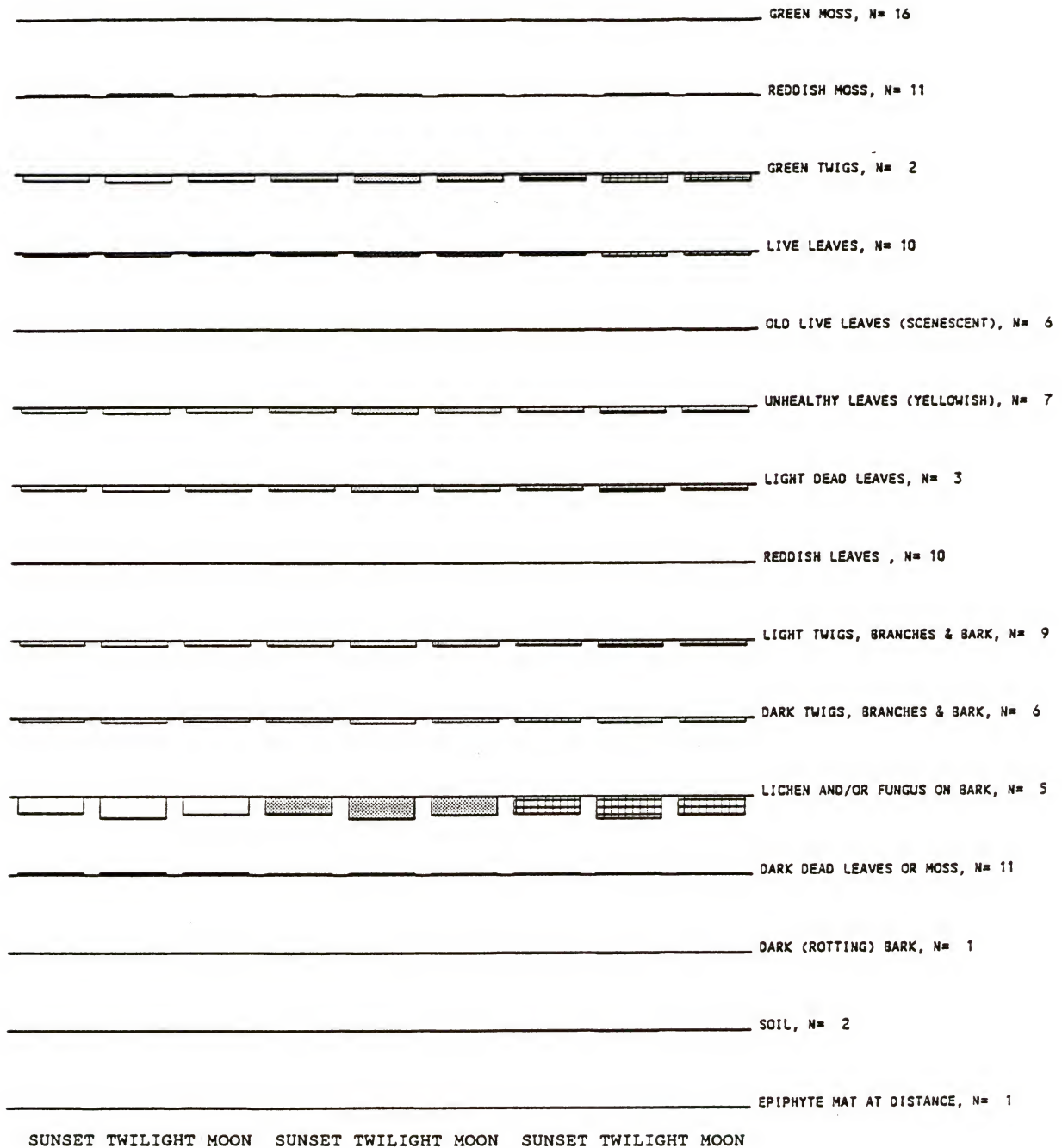
Figure 4-11--continued

E. Scotinomys teguina



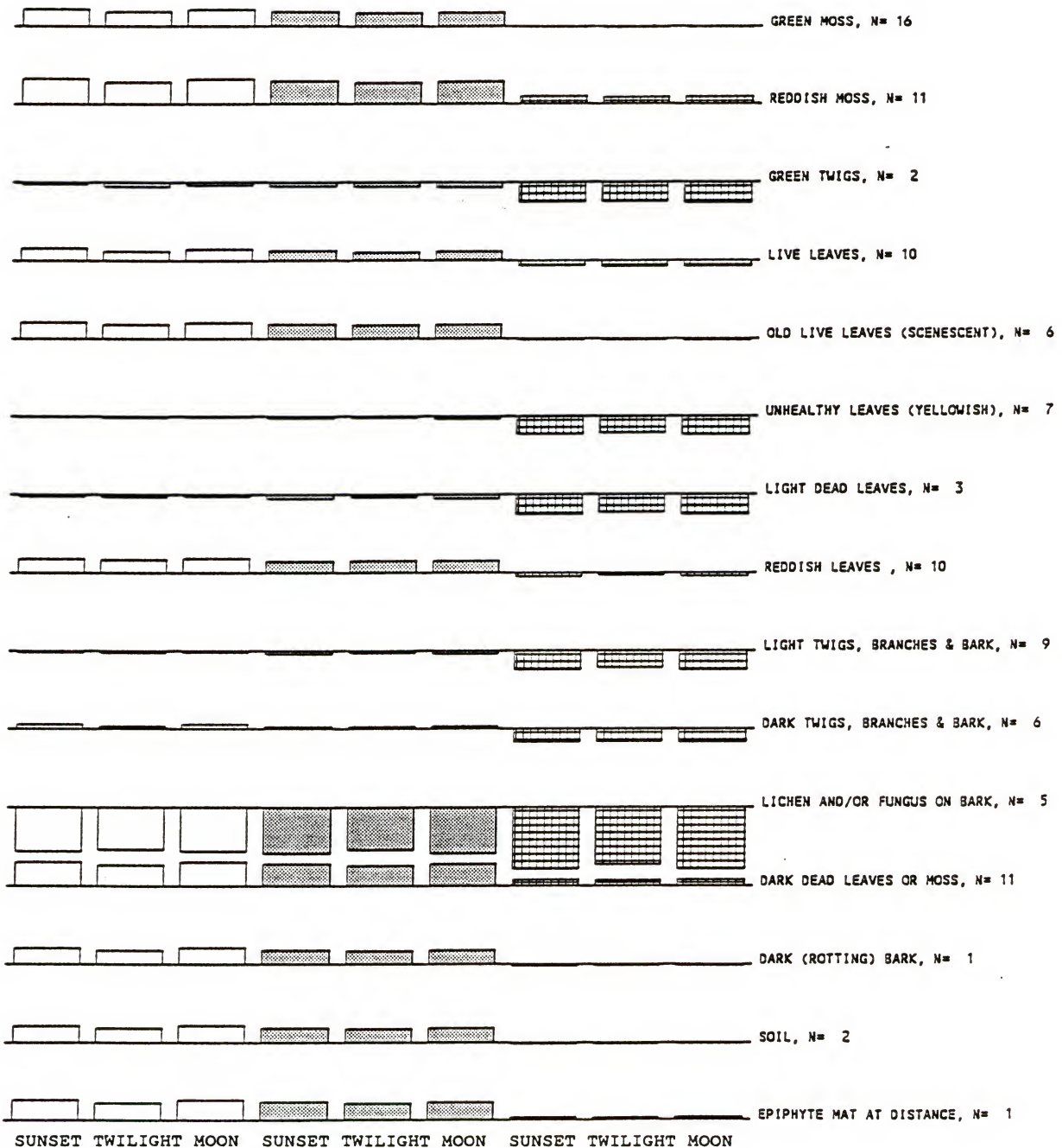
CALCULATED BRIGHTNESS DIFFERENCES
WITHOUT EFFECTS FROM ROD VISION

Figure 4-11--continued

F. Scotinomys teguina

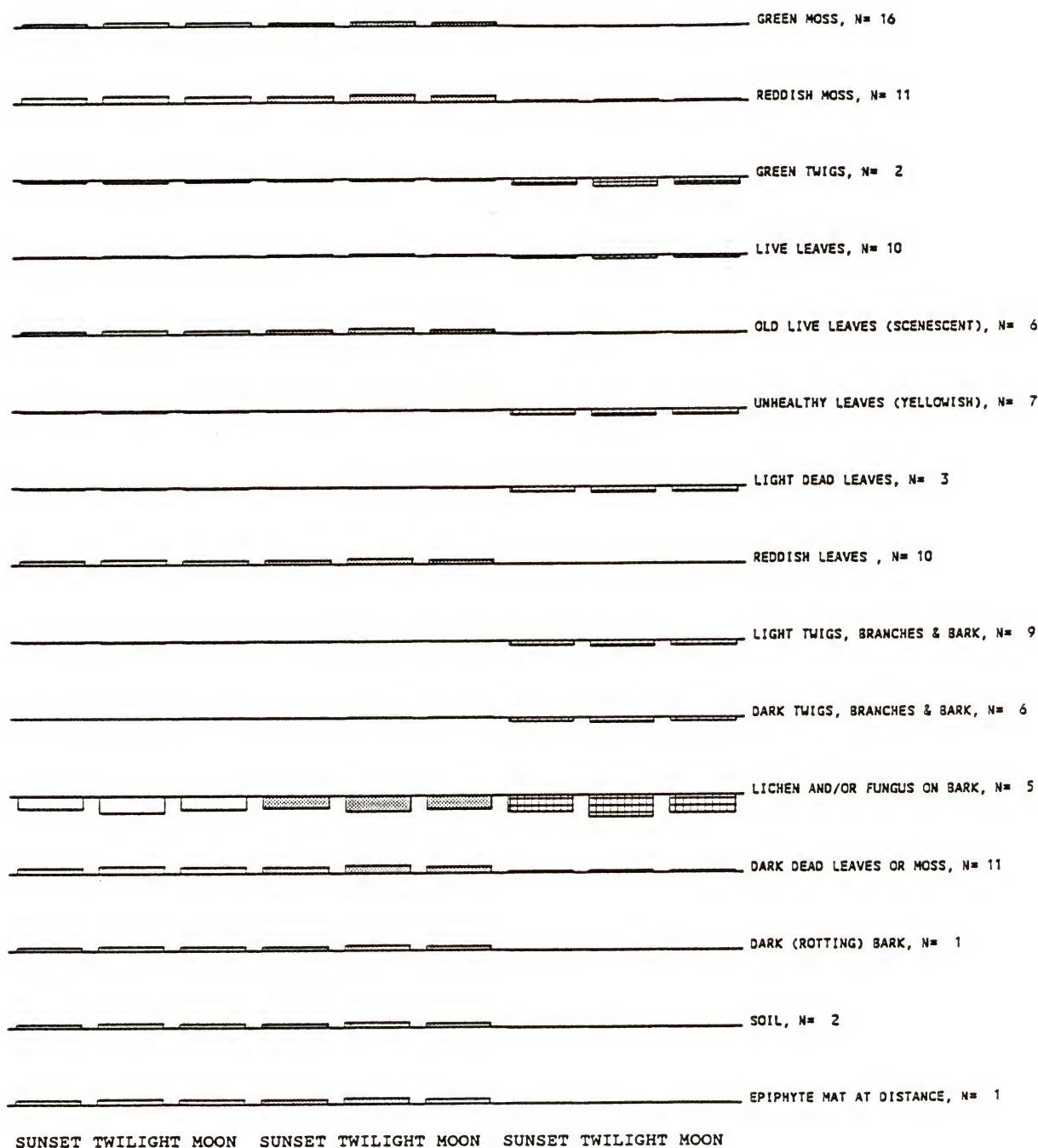
CALCULATED BRIGHTNESS DIFFERENCES
UNDER ROD VISION

Figure 4-11--continued

G. Peromyscus nudipes

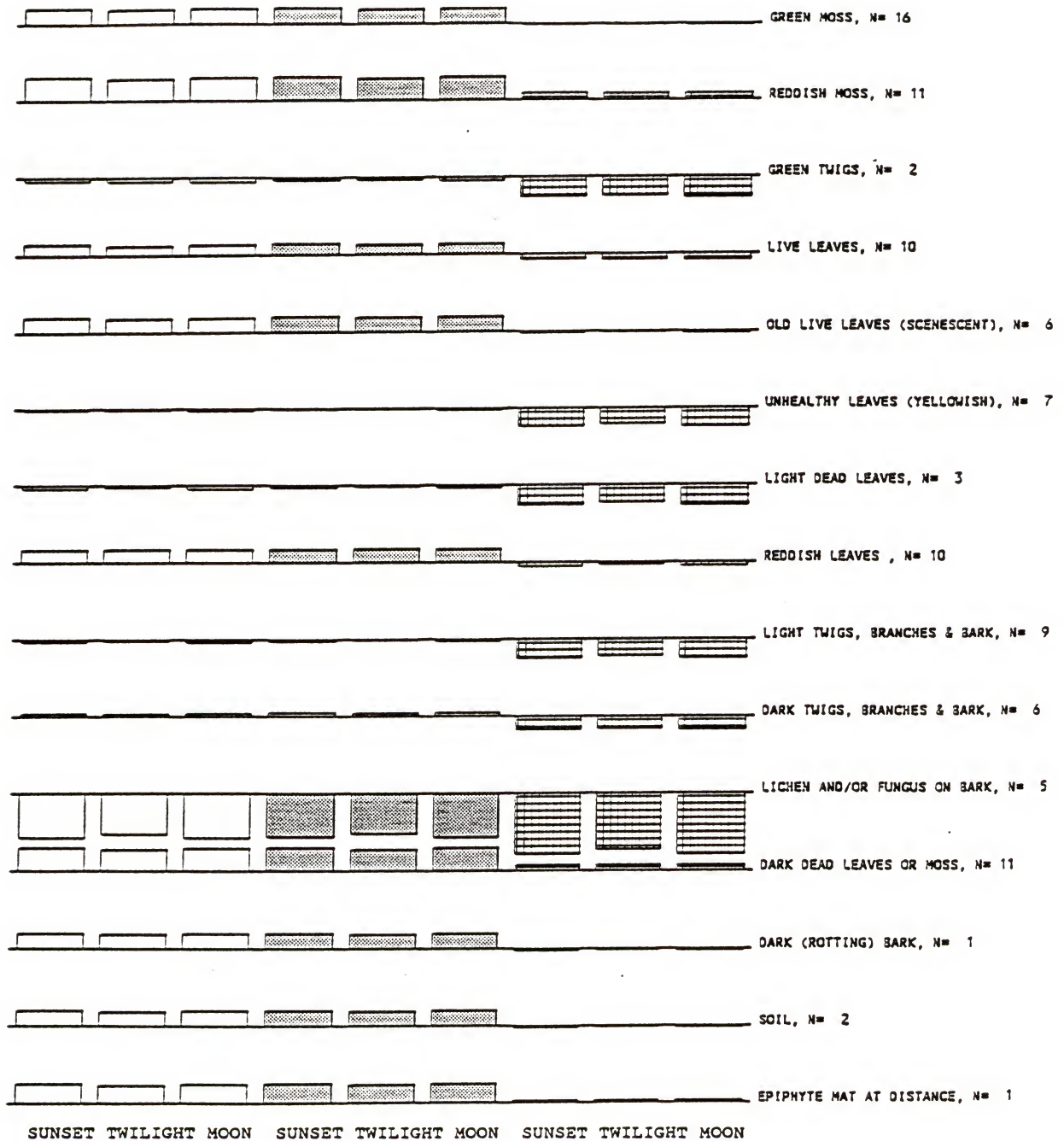
CALCULATED BRIGHTNESS DIFFERENCES
WITHOUT EFFECTS FROM ROD VISION

Figure 4-11--continued

H. Peromyscus nudipes

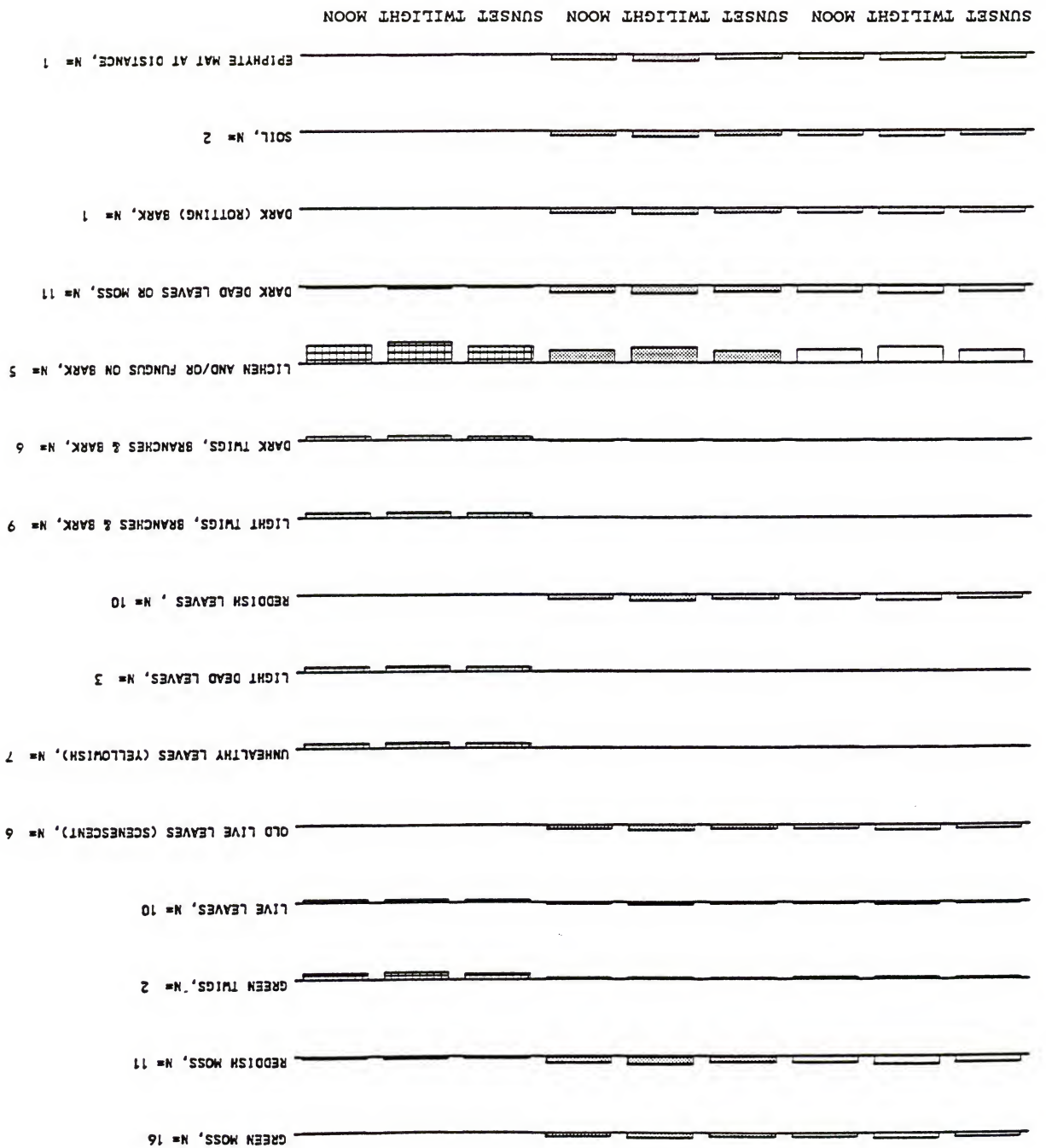
CALCULATED BRIGHTNESS DIFFERENCES
UNDER ROD VISION

Figure 4-11--continued

I. Heteromys desmarestianus

CALCULATED BRIGHTNESS DIFFERENCES
WITHOUT EFFECTS FROM ROD VISION

Figure 4-11--continued



CALCULATED BRIGHTNESS DIFFERENCES
UNDER ROD VISION

particularly when the back was viewed. It was a fairly close match to green as well as reddish leaves. The flank in all species was consistently brighter than most backgrounds. The terrestrial species, S. teguina, P. nudipes, and H. desmarestianus, all made fairly close matches to soil and dark rotting bark. However, the diurnal S. teguina was the only species to match brightness on all three dorsal areas of the body. Only spectra from the back of both P. nudipes and H. desmarestianus closely matched the brightness of soil and dark rotting bark.

Discussion

General Patterns of Coloration

Two prominent patterns emerged from the analysis of color reflectance in the five species of mice (Table 4-1). First, hue shows little variation among species and individuals, while brightness and chroma show a broad range of values. Second, pelage spectra appear to cluster in species-typical patterns that may be indicative of vertical specialization.

The small differences in hue could indicate a selective regime common to all the species, but physiological constraints could also be involved. Pelage color in all mammals is dependent on the presence or absence of melanin granules in the cortex and medulla of individual hairs. There are two distinct forms of mammalian melanin that differ in color; eumelanin is brown or black, whereas pheomelanin is yellow or reddish (Searle, 1968). The acquisition of additional coloration pigments through feeding does not occur in mammals. Vertebrates and invertebrates in general cannot synthesize carotenoids, but many species, excluding mammals, obtain these pigments from plants and often sequester pigments in plumage or integument (Rothschild, 1975). Structural colors, such as the iridescence of hummingbird feathers, produced by the reflecting properties inherent to the structure of the

Table 4-1. Summary chart of the results of the coloration analysis.

SPECIES	VERTICAL SPECIALIZATION	HUE	CHROMA RANK (1=lowest, 5=highest)	BRIGHTNESS RANK (1=lowest, 5=highest)
<u>Scotinomys</u> <u>teguina</u>	terrestrial	orange/ yellow	3	1
<u>Heteromys</u> <u>desmarestianus</u>	terrestrial	orange/ yellow	2	3
<u>Peromyscus</u> <u>nudipes</u>	scansorial	orange/ yellow	1	2
<u>Reithrodontomys</u> <u>gracilis</u>	arboreal	orange/ yellow	5	4
<u>Nyctomys</u> <u>sumichrasti</u>	arboreal	orange/ yellow	4	5

reflecting surface, are limited to only a few species of mammals and are restricted to naked epidermis, not fur (for example, the bright blue face of the mandrill) (Searle, 1968). Thus, pelage color in mammals is primarily a function of the distribution and proportion of these two melanins within the individual hair coupled with the distribution of differently colored hairs over the body. This restricts hues to the red/orange portion of the spectrum.

So, why are mammals orange/yellow? Does the color have an adaptive function under nocturnal conditions that might explain the origin of the two pigment system? The results of these analyses provide no obvious and plausible adaptive explanations. Changes in appearance of pelage as a consequence of the reddish color of low-level light environments and spectral sensitivity of rod cells, coupled with the origin of mammals from a nocturnal ancestor, suggest that hue may be, or once was adaptive. It is not clear, however, why mammals are not variable in hue, matching the hue of the background. In addition, adaptive explanations are lacking for the evolution of vertebrate rod pigments that are maximally sensitive to green wavelengths close to 507 nm (for a review see Goldsmith, 1990). It has been suggested by vision physiologists that sensitivity may have evolved to take advantage of reflections from green plants, but plants have a peak reflectance closer to 550 nm and not the 507 nm of rhodopsins. Another explanation proposed is that since night-vision is sensitive to single photons of light, sensitivity to longer wavelengths that more closely match the color of ambient light at those times would be jeopardized by background noise from photons generated from body heat. Physiological analyses at the molecular level, however, have not clearly demonstrated such interference. Phylogenetic inertia also has been suggested, but crustacea, which are not closely related to vertebrates, have rhodopsins that are also sensitive to the same range of wavelengths as vertebrates, suggesting convergence under a common selective regime. As Goldsmith

(1990, p.298) stated, "We are clearly missing something important." Perhaps once we gain an understanding of the visual function and evolution of scotopic pigments, the origin of reddish-orange coloration in mammals may become clear.

Although the mice of the cloud forest community show little variation in hue, there is considerable variation among species and individuals in the other two characters, brightness (Figure 4-4) and chroma (Figure 4-5). Previous studies of pelage color in terrestrial nocturnal mice support an adaptive hypothesis of background matching for brightness. Studies of geographic variation in beach mice (Sumner, 1926) and desert rodents (Benson, 1933; Dice and Blossum, 1937) demonstrated that populations tend to match the brightness of the sand, soil, or lava flows of the habitat. Semi-natural (Brown, 1965; Kaufman and Wagner, 1973) and captive experiments (Dice, 1947; Kaufman, 1974) with mice and predators demonstrated that visual predators more frequently prey on mice that differ in brightness from backgrounds.

A functional explanation for differences in chroma may lie in the limitations of the mammalian pigmentation process. Pigment deposition of eumelanin and phaeomelanin is genetically controlled by multiple loci that affect which of the two types of melanin are deposited in pigment granules, and the number, shape, arrangement, or position of the granules (Searle, 1968). Dark pelage is dominated by hairs with black eumelanin and has low chroma; brighter pelage is dominated by hairs with the reddish phaeomelanin and has higher chroma. The brightest pelage (with low chroma) is white dominated by hairs containing air space rather than pigment. Gray pelage contains a combination of pigments and air space. Thus, because of the two-pigment system, there are only two means by which pelage can become brighter: either increase the amount of phaeomelanin or decrease the amount of pigment deposited. The pelage of the arboreal mice of Monteverde are rich in phaeomelanin, so the question that arises is why are they not gray? Since pigment deposition

is under at least partial genetic control (Searle, 1968), natural selection from visual predators can act to increase or decrease in the population the frequency of the color morphs that differ in brightness. Which color morphs predominate will depend on the ambient light and background colors at the time and place where the animals are most subject to predation.

Coloration and Temporal Specialization

There are three periods in the 24 hour day with very distinct light regimes by which animals are viewed: day, night, and twilight. Day is marked by light regimes of bright intensities and hues of white, green, or blue-gray; night and twilight are marked by low light intensities and hues of reddish or purplish (Figure 4-2). Changes in hue and chroma of ambient light between these periods affected the calculated brightness of reflectance spectra (Figures 4-8 and 4-9; Endler, 1991). The changes in brightness are small, but the response of the visual system to these differences may not be, particularly under rod vision at low light intensities.

In contrast to the small changes in calculated brightness of spectra by the color of ambient light, the spectral sensitivity of rod cells substantially changed the calculated perceived brightness of spectra (Figures 4-10 and 4-11) and most likely affects brightness perception by nocturnal predators. Objects of quite different hue and brightness during daylight (such as green twigs and red mouse pelage) may be equivalent in perceived brightness at night. The results verify that color is an important factor in visual perception at night, and should be included in models assessing visual crypsis in nocturnal animals.

The color of light in forests under the low-light conditions after twilight are not known because of limitations in the sensitivity of spectroradiometers. Reflectance from vegetation may affect the spectrum

of incident light entering the canopy, and affect the perception of brightness contrast. Nevertheless, several lines of evidence suggest that nocturnal predation based on vision is greatest under twilight and moonlight, conditions for which we have adequate spectral measurements for analyses. Twilight is a period of overlap in the activity patterns of both diurnal and nocturnal predators. Most owls and forest falcons are crepuscular foragers (Martin, 1990; Stiles et al., 1989), and captive and field studies of felids, mustelids, and canids have shown that many mammalian carnivores extend their diurnal or nocturnal activity patterns to include twilight (Emmons et al., 1989; Kavanau, 1971; Konecny, 1989; Sunkist, et al., 1989). Recent studies of visual acuity in owls and cats show that the ability to detect brightness contrast falls substantially at low light levels (Martin, 1990) and that on moonless nights the light beneath the forest canopy is insufficient for visual foraging by birds. Hearing and olfaction predominate under these conditions and are adequate for foraging by sedentary and territorial individuals that are extremely familiar with the landscape (Martin, 1990). These sensory findings are supported by differences in the behavioral patterns of nocturnal prey and predators at different light levels. Many species of bats and rodents are lunar-phobic, decreasing activity in open areas under bright moonlight, suggesting that the behavior evolved in response to greater predation under brighter light (Emmons et al., 1989; Kotler, 1984).

The trapping study (Chapter 2) identified one diurnal and four nocturnal species. The sample size is not large enough to identify any trends in color patterns but provides data for future comparison with other species. When the diurnal S. teguina is compared to its nocturnal counterparts, three differences are found regarding the color of the pelage: 1) The diurnal species is darker. 2) Differences in brightness between the body parts are less in S. teguina than in the others; the nocturnal species all show highly reflective spectra on the flanks and

venters. 3) When compared to its terrestrial counterparts, P. nudipes and H. desmarestianus, the diurnal species has higher chroma compared to the gray species.

Coloration and Specialization for Vertical Habitats

When the nocturnal arboreal species are compared to their nocturnal terrestrial counterparts, two patterns emerge: standardized reflectance spectra are brighter in the arboreal species and they have greater chroma (Table 4-1). When pelage spectra are compared to backgrounds in the habitat under the various light conditions, the results suggest that the differences in color among species may be a consequence of selection for brightness matching. The mean spectra for R. gracilis and N. sumichrasti appear to be more cryptic against backgrounds found in arboreal strata and are not particularly good matches to soil and rotting bark found on the forest floor. The mean spectra of the two terrestrial species show the reverse pattern and are most cryptic on soil. Peromyscus nudipes, primarily terrestrial but with arboreal behavior that varied both among individuals and over time (Chapter 2 and 3), interestingly shows the greatest range of variation in brightness and chroma and appears to be polymorphic in its color patterns. Polymorphic characters often arise in populations subject to multiple selective regimes acting on the same character (Futuyma and Moreno, 1988).

Is Pelage Color an Adaptation for Vertical Specialization?

The analyses of the data suggest that selection by visually hunting predators for brightness matching of pelage to background has occurred in the Monteverde community of mice in association with vertical specialization. Well-defined brightness matches, however, were not clearly demonstrated and additional study is required to further evaluate the function of pelage color in nocturnal forest-dwelling mice.

Comparative study of other forest rodent communities is obviously necessary to confirm or reject the patterns discerned in the Monteverde community. However, reevaluation of the data using calculations that model additional variables may also prove fruitful. The importance of the sensitivity curve of rod cells in approximating visual perception of nocturnal predators was apparent from the results, decreasing the calculated discrepancy in brightness between pelage and backgrounds. The color of the ambient light reflected from the pelage also affected the appearance of spectra, although the magnitude of these effects on perception awaits investigation by physiologists and psychobiologists. Other characters and variables, however, are most likely important, and further analyses are required to construct more realistic models that approximate perception in nocturnal predators.

Three factors should be considered for inclusion in later models. First, the ability to detect contrast differences between prey and background falls substantially at low light levels (Martin, 1990), and at some threshold, light is insufficient for visual foraging. Light attenuates along the vertical profile of a forest, and arboreal mice active in light regimes of greater intensity may experience stronger selection for brightness matching than terrestrial mice active on the relatively darkly-lit forest floor. Second, perception at twilight may be influenced by effects due to the transitional process from color vision to night vision. Mesotopic vision during this transition is achieved by the stimulation of both rod and cone cells, the red cones being the last photopic cells to function. There may be effects produced by the interaction of the two visual systems (John A. Endler, pers. comm.), an important consideration that may help to answer the question why the arboreal species are yellow-orange rather than light gray in color. Third, the appearance of background spectra changes with wet and dry conditions. The effect of this color change on selection for background matching may be substantial, as suggested by a

biogeographic color trend common among vertebrates and invertebrates known as Gloger's rule (Mayr, 1963; Rensch, 1960; Zink and Remsen, 1986). Pigmentation is generally heavy in warm humid areas but reduced in cool dry areas. The adaptive significance of this color pattern is unknown (Mayr, 1963).

Close matches between pelage and specific backgrounds in the habitat, predicted from a hypothesis of selection for crypsis, however, may not necessarily be expressed in the populations examined. Multiple selective regimes can affect pelage color, and these regimes can act in consort or in opposition. Animals live through 24 hour cycles that encompass a variety of activities in ever changing light environments, against a variety of color backgrounds and visual predators; selection will vary depending on conditions (Endler, 1991). Under what conditions each species encounters the most intense predation (diurnal nest sites, twilight foraging, or while signalling to conspecifics?) is unknown. The species examined are found not only in cloud forest, but in a diversity of habitats within a broad geographic range (Chapter 1). Selection is most likely different in each habitat type, and gene flow from immigrating individuals can dilute the effects of local selection (Thompson, 1990).

Despite these caveats, perceptual and neurological processes being explored by psychobiologists and vision physiologists suggest that selection should be strong for brightness matching of prey and backgrounds. These processes are being studied primarily in primates and humans, but may be common to several, if not all, vertebrate visual systems (Goldsmith, 1990).

Ramachandran (1988a; 1988b) studied the human visual system and the perception of three-dimensional shapes from shading. He discovered several computational rules that the brain uses to discern depth and solidity. First, three-dimensional shapes are perceived only if the borders of the object are defined by differences in brightness to the

background. Differences in color are not used in the detection of solid form (Ramachandran, 1988a). If the borders of an object match the brightness (luminance) but not the color of the background, its three-dimensional nature disappears to the viewer. Second, the detection of shape and depth is a prerequisite for the perception of motion (Ramachandran, 1988b). The human brain evidently functions by a hierarchy in computational rules and first must recognize shape before it can perceive apparent motion. Third, detecting shape from shading is constrained by an inherent assumption that only one light source illuminates the entire visual field (Ramachandran, 1988a). An object that appears to be illuminated from a light source different in orientation from the light illuminating the other objects in the image is incongruous with its surroundings and is not perceived as having depth. It must be viewed separate from the others before the depth of its form appears.

If these findings hold for other visual systems, they may explain an adaptive advantage to diurnal as well as nocturnal animals in matching coloration to the brightness of the background; form as well as motion may be obscured long enough to evade predation. The assumption of one light source in discerning shape also offers an alternative explanation for the evolution of countershading, a color pattern exemplified by many arboreal mice in which dark pigmentation occurs on body parts exposed to illumination (the dorsum) and light pigmentation occurs on parts shaded from illumination (the venter). The historical interpretation of this pattern is that countershading obliterates the natural shading effects by which a predator can detect shape and form (Cott, 1940; Thayer, 1909). Kiltie (1988) pointed out that for maximum effect countershading should occur with a gradation of pigmentation from dorsum to venter, but often in terrestrial organisms the change is abrupt. The sharp contrast of light and dark pigment actually enhances contrast, but if the effect is such that it appears the animal is

illuminated by a light source that is counter to the light within the habitat, the animal will be incongruous with its surroundings and may evade detection altogether.

The universal nature of forest light environments (Endler, in press), the restriction of most mammal coloration to patterns produced by two pigments (Searle, 1968), the universal use in vertebrate night-vision of rod cells with a characteristic sensitivity curve (Goldsmith, 1990), and the green and brown backgrounds common to all forests suggest that common selective regimes and evolutionary processes affect the evolution of pelage color in most nocturnal forest-dwelling mammals. Further comparative studies hold promise in elucidating general patterns, processes, and functions involved in the evolution of adaptive coloration in mammals.

CHAPTER 5 CONCLUSIONS

The results of the three comparative studies (Chapters 2, 3, and 4) show that there is a suite of potentially adaptive characters associated with vertical habitat specialization in the cloud forest community of mice (Tables 5-1, 5-2, 5-3). These characters include both behavior and coloration. Analyses of behavior were particularly revealing because vertical specialization for each species resulted as a direct consequence of behavior. The two different approaches I used to study behavior--the trapping study and the escape response experiments--give different insights into both proximate and ultimate mechanisms of vertical specialization.

In the trapping study, I examined the natural variation in behavior that occurred within the habitat. There were species-typical vertical distribution patterns, as well as species-typical behavior patterns that underlaid the distributions (Table 5-1). Because the study was conducted under natural conditions, these patterns are indicative of ecological specialization after the influence of external factors in the environment, such as competition, predation, resource fluctuations, etc. are taken into account (Futuyma and Moreno, 1988; Partridge, 1978). Thus the results of this study must be interpreted first in terms of proximate mechanisms that can account for the observed patterns of vertical specialization within this particular community.

Based on the frequencies of capture of individuals among the vertical habitats sampled, two types of behavior appear to define vertical specialization within the community: 1) preference for activity in one particular vertical stratum over another, and 2) fidelity to that

Table 5-1. Summary chart of the distribution and behavior patterns described by the results of the trapping study (Chapter 2).

SPECIES	DISTRIBUTION	HABITAT PREFERENCE	VARIATION AMONG INDIVIDUALS	FACULTATIVE CHANGES OVER TIME	SPECIALIZATION
<u>Scotinomys</u> <u>teguina</u>	forest floor	forest floor	no	no	specialized terrestrial
<u>Heteromys</u> <u>desmarestianus</u>	forest floor	forest floor	no	no	specialized terrestrial
<u>Peromyscus</u> <u>nudipes</u>	forest floor understory	forest floor	yes	yes	generalized terrestrial
<u>Reithrodontomys</u> <u>gracilis</u>	forest floor understory crowns	understory crowns	yes	no	generalized arboreal
<u>Nyctomys</u> <u>sumichrasti</u>	understory crowns	crowns	?	yes?	specialized arboreal

preferred stratum. Heteromys desmarestianus and S. teguina are terrestrial specialists. They were exclusively active in only one stratum, and individuals showed no variation in vertical activities through time. In contrast, P. nudipes and R. gracilis were active in more than one stratum, and there was variation both among and within individuals in vertical activity. The species are more generalized in their use of vertical habitats than the exclusively terrestrial species, but the narrow range of variation among individuals indicates that they had a preference for activity in one stratum. Trapping data are limited for Nyctomys sumichrasti, but the lack of captures on the forest floor, and trapping studies by other investigators (Ceballos, 1990; Fleming, 1970), indicate that the species is an arboreal specialist.

Several external factors in the environment appeared to affect behavioral fidelity in some, but not all of the species. The concentrated number of captures of N. sumichrasti in the lower understory during a brief time period may have been indicative of a facultative shift in activity due to food shortage in higher strata where it normally forages. Similar shifts in activity as a result of a resource shortage been documented for a Panamanian population of this species (Fleming, 1970). Changes in the vertical distribution patterns of P. nudipes were associated with changes in the population levels within the community. However, further study is needed to establish if population and/or community dynamics was the primary cause of this shift. Density-dependent effects on habitat selection and microhabitat specialization are currently receiving considerable attention from population ecologists (Morris, 1989; Rosenzweig, 1991).

Differences among the five species in their response to external factors in the environment are not surprising. The results confirm the findings of other investigators who have conducted trapping studies of other mammal communities (Fleming, 1970; Harney and Dueser, 1987; Holbrook, 1979; Kotler, 1984). Some species respond to changing

pressure from predation, competition, or resource abundance with facultative changes in behavior; some species do not. Plasticity in behavior may be an important adaptive character for species that inhabit forests subject to degradation and/or fragmentation from human encroachment. Studies of behavioral plasticity and the ecological pressures that affect changes in behavior may, and should, become more important in the field of conservation biology.

Comparisons of trapping frequencies in arboreal and ground traps also revealed that, at least for P. nudipes, previous experience can modify behavior and affect vertical activity patterns. First captures of individuals of P. nudipes in which the animal had the opportunity to enter either a ground or arboreal trap were always in ground traps. It was only after a first experience that individuals were captured off the ground. This experience effect is often viewed as a "nuisance" by population biologists who must contend with variation in capture probabilities in statistical models used to estimate population size (Lebreton et al., 1992), but such an effect may be indicative of adaptive behavior. One hypothesis that could be tested is that P. nudipes will harvest ripe fruit from understory shrubs, but only after encountering fallen fruit on the forest floor. Unfortunately, effects of learning on behavior are more easily identified in captive studies than in field studies. An awareness by field biologists that patterns indicative of learning may emerge from field data could help to identify hypotheses that can then be tested in captive or semi-natural experiments.

The trapping study identified several proximate mechanisms that influence vertical specialization in the community, but my original interest in terrestrial and arboreal specialization centered on the role of vertical specialization in the adaptive radiation of murid rodents (Chapter 1). Questions concerning evolution require a study of inherited characters rather than a study of variation due to proximate

external factors in the environment. Futuyma and Moreno (1988) suggested that evolutionary questions should center on genetic changes in behavior, because behavior is often the mechanism by which specialization is exercised, and behavior often defines the selective pressures to which the individual is subject.

Results of the trapping study identified habitat preference and fidelity to the preferred stratum as behavior that best describes the observed patterns of vertical specialization. I believe that the series of escape response experiments, in which external variables could be controlled, provided a means of measuring such behavior that could prove useful in comparative studies of other forest-dwelling species.

The results of the experiments (Table 5-2) showed consistent decisions among individuals within a species to climb or not to climb. Decisions of individuals released on the ground and on the vertical T-maze were consistent with the vertical habitat preferences of each species shown in the trapping study. The results of the angled Y-maze experiment demonstrated that habitat preference could be over-ruled in some individuals by factors external to the animal, and this was consistent with the variation in climbing activity shown by each species during the trapping study. The two species that showed variation in their frequency of capture among arboreal and ground traps (*P. nudipes* and *R. gracilis*) showed significant differences in their escape response on the two apparatuses. *Scotinomys teguina*, however, which was exclusively captured in ground traps and did not vary its vertical activity in the trapping study, did not show a significant difference in its escape response between the two experiments. Its preference for the forest floor was very strong and difficult to over-rule by the difficulty of the escape route.

The behavior patterns identified in the escape response experiments corroborate the species-typical behavior patterns that were expressed in the trapping study. Because the experimental design placed

Table 5-2. Summary chart of the results of the escape response experiments (Chapter 3).

SPECIES	VERTICAL SPECIALIZATION	ESCAPE ON GROUND RELEASE	ESCAPE ON HORIZONTAL ARM	ESCAPE AT ON VERTICAL T-MAZE	ESCAPE ON ANGLED Y-MAZE
<u>Scotinomys</u> <u>teguina</u>	terrestrial	forest floor	run	climb down	climb down
<u>Heteromys</u> <u>desmarestianus</u>	terrestrial	forest floor	jump	jump down	?
<u>Peromyscus</u> <u>nudipes</u>	scansorial	forest floor	run/jump	climb down	climb up
<u>Reithrodontomys</u> <u>gracilis</u>	arboreal	forest floor understory	run/jump	climb up	climb down
<u>Nyctomys</u> <u>sumichrasti</u>	arboreal	understory	?	?	?

the species-typical disposition or preference for a particular stratum in direct conflict with a difficult climb on a standardized structure, my interpretation is that the results are indicative of fundamental behavior patterns that closely reflect the genetic properties of the individual. Further analyses are required to verify this interpretation. Nevertheless, based on the available evidence, I propose the hypothesis that climbing disposition is the fundamental behavior by which vertical specialization is achieved in the Monteverde populations, and that generalized behavior is a consequence of the ability of additional factors to over-rule that basic disposition.

The hypothesis must be tested in other communities, and the genetic basis of the behavior must be established. If the hypothesis is supported, however, there is the opportunity to pose and answer some basic questions as outlined by Futuyma and Moreno (1988) concerning the evolution of specialization. Consequences of genetic changes in behavior could be examined if disposition is a fundamental behavior on which selection acts to produce vertical specialization. The role that learning plays in the expression of specialization could also be studied. Wecker (1963) demonstrated genetic differences in individual preference for grassland habitats or woodland habitats between two races of Peromyscus maniculatus. He found that the preference could be reinforced by experience in the preferred habitat, but not reversed by experience in the less preferred habitat. Similar studies could be conducted concerning habitat selection along the vertical profile. In addition, conflict experiments similar to the maze experiments could provide a quantitative means of measuring and comparing specialization among populations and species. If behavioral character states can be identified for different populations or species independent of confounding factors in the environment, phylogenetic analyses are possible, with the exciting possibility of examining the evolution of

vertical habitat specialization within the adaptive radiation of murid rodents.

Behavioral specialization to particular vertical strata will influence the evolution of morphological and physiological adaptations because selective regimes are encountered as a consequence of habitat selection (Endler, 1992; Futuyma and Moreno, 1988). The evolution of locomotor morphology that reduces the likelihood of falling is a common example of morphological adaptation as a consequence of climbing behavior (Cartmill, 1974; 1985). The results of the coloration analysis presented in Chapter 4 suggest that other morphological adaptations have evolved as well. There appears to be an association of pelage coloration with vertical habitat specialization in the rodent community at Monteverde (Table 5-3). Arboreal specialists are more highly reflective than terrestrial specialists, which are dark. All species are orange/yellow in hue, but arboreal species have higher chroma and appear more orange than terrestrial species which have low chroma and an orange cast to their gray fur. The analyses suggest that to nocturnal visual predators arboreal species appear to match the brightness of the backgrounds in arboreal habitats; terrestrial species appear *****to match the brightness of the dark backgrounds of the forest floor. The arboreal species are brighter primarily because the high chroma of their pelage strongly reflects the orange/red light found in nocturnal environments. Further analyses are required to test these hypotheses and test for similar color patterns in other rodent communities. The coloration analyses also suggests that visual perception of the nocturnal predators most likely affects the appearance of mice against the backgrounds of the habitat, and will in turn influence the evolution of color patterns (Endler, 1991; Endler, 1992). The impact of perceptual abilities and constraints imposed by the sensory systems of organisms on the process of sexual selection and the evolution of signals is a growing field of study (Endler, 1991; 1992; Ryan, 1990;

Table 5-3. Summary chart of the results of the coloration analysis (Chapter 4).

SPECIES	VERTICAL SPECIALIZATION	HUE	CHROMA RANK (1=lowest, 5=highest)	BRIGHTNESS RANK (1=lowest, 5=highest)
<u>Scotinomys</u> <u>teguina</u>	terrestrial	orange/ yellow	3	1
<u>Heteromys</u> <u>desmarestianus</u>	terrestrial	orange/ yellow	2	3
<u>Peromyscus</u> <u>nudipes</u>	scansorial	orange/ yellow	1	2
<u>Reithrodontomys</u> <u>gracilis</u>	arboreal	orange/ yellow	5	4
<u>Nyctomys</u> <u>sumichrasti</u>	arboreal	orange/ yellow	4	5

Ryan and Rand, 1990). Differences in perception and information processing among populations also have an impact on the evolution of behavior associated with ecological specialization (Greenberg, 1983; 1990), but have received less attention. Futuyma and Moreno (1988) described constraints from perception and information processing as an important aspect of ecological specialization requiring further study. The trapping and maze experiments suggest that vertical specialization among the mice in Monteverde may be due to differences in the way in which they process, perceive, and respond to information from the environment. Further investigation of perceptual differences among the species could potentially yield a great deal of information on how and why species are adapted for specialization in different vertical strata of the forest.

Further studies of nocturnal climbing mice should provide new insights about vertical habitat specialization and the evolution of adaptations associated with specialization. The behavior and coloration patterns presented here are only a few of many potential adaptations that contribute to the ability of mice to live in forests. Because of their non-flying and predominantly nocturnal nature, tactile, olfactory, and auditory cues are most likely the basis for assessing and choosing habitats. Mice should perceive and react to their environment in ways not displayed by diurnal species, and herein lies the challenge for future studies of the evolution of adaptations for vertical specialization in mice.

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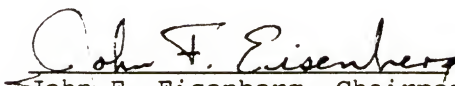
BIOGRAPHICAL SKETCH

Catherine Ann Langtimm was born 28 April 1952 to Edna Ann Eggemann and Duane Harry Langtimm in Davenport, Iowa. Her early education was in Davenport where she attended Assumption High School, and in 1974 graduated with the Bachelor of Science degree from St. Ambrose College.

After graduation she moved to Washington, D. C. and began a career with the U. S. Fish and Wildlife Service as a museum specialist in the Bird and Mammal Laboratory at the U. S. National Museum. It was there she learned to trap mice, net bats, prepare museum study skins, and maintain the curatorial standards of a vertebrate museum collection. Working in that venerable collection she first saw the diversity of organisms and the complexity of their evolution and adaptive radiation. In the museum and in the field she was trained in the philosophy and classical traditions of the early naturalists and mammalogists of the Biological Survey.

She made her first trip south of the Tropic of Cancer in 1977 on a collecting trip to Nayarit, Mexico. Her interest in the tropics solidified during a course with the Organization for Tropical Studies in 1983. In August of 1984, she completed her Master of Science degree in the Biology Department at George Mason University, Fairfax, Virginia. She began her work in the Zoology Department at the University of Florida in 1985. She plans to continue her work on adaptations and specialization in rodents and hopes to contribute to the fields of conservation and education.

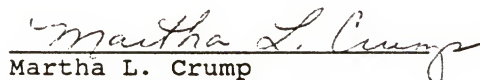
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John F. Eisenberg, Chairperson
Katharine Ordway Professor of
Ecosystem Conservation


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H. Jane Brockmann
Professor of Zoology

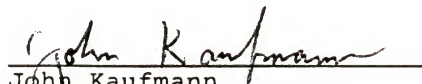
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Martha L. Crump
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


John J. Ewel
Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.


John Kaufmann
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



Richard A. Kiltie
Associate Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May 1992

Dean, Graduate School